

I 29.80:13

Clemson University



3 1604 019 680 687


GOVT. DOCUMENTS  
DEPOSITORY ITEM

NOV 3 1980

CLEMSON  
LIBRARY

# THE IMPACT OF THREE EXOTIC PLANT SPECIES ON A POTOMAC ISLAND





Digitized by the Internet Archive  
in 2012 with funding from  
LYRASIS Members and Sloan Foundation

# THE IMPACT OF THREE EXOTIC PLANT SPECIES





# THE IMPACT OF THREE EXOTIC PLANT SPECIES ON A POTOMAC ISLAND

Lindsey Kay Thomas, Jr.  
Research Biologist  
National Park Service

National Park Service Scientific Monograph Series • Number Thirteen • 1980

U.S. Department of the Interior

*As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in Island Territories under United States administration.*

#### **Library of Congress Cataloging in Publication Data**

Thomas, Lindsey Kay.

The impact of three exotic plant species on a  
Potomac island.

(National Park Service scientific monograph; no. 13)

Bibliography: p.

Includes index.

1. Botany—Washington, D.C.—Ecology. 2. Theodore  
Roosevelt Island, D.C. 3. *Hedera helix*. 4. Japanese  
honeysuckle. 5. *Iris pseudacorus*. 6. Weeds—Wash-  
ington, D.C. 7. Plant introduction—Washington,  
D.C. I. Title. II. Series: United States. Nation-  
al Park Service. Scientific monograph series; no. 13.  
QK153.T46 581.5'24 77-608164

# *Contents*

ACKNOWLEDGMENTS    xiii

SUMMARY    xv

Chapter 1

INTRODUCTION    1

    The General Problem    1

    Location and Physical Description of Study Area    1

    Summary of Human History and Past Land Use    3

    Vegetation of the Study Area    3

    The Species Selected for the Study    4

    The Purpose of the Study    5

Chapter 2

MATERIALS AND METHODS    7

    Design of Observations and Statistics    7

    The Physical Setup (Materials)    8

        The habitats studied    8

        The placement of 1 × 1m quadrats    9

        The placement of light stations    10

        The placement of vegetational strata stations    12

        The placement of elevation stations    12

        The competition experiments    12

        The germination observations    12

        The controlled shade and light experiments    13

        The censuses    13

    The Observational Methods    13

        Control check    13

        Importance of the exotics in different habitats    14

        Replacement of one species or life form by another    20

        Limiting factors    24

    Miscellaneous Observations    32

Chapter 3

RESULTS    33

    Importance of the Exotics in Different Habitats    33

        Ecological dominance    33

        Growth rate    34

        Importance of English ivy on the flood plain    34

Replacement of One Species or Life Form by Another	35
Replacement of native life forms and species	35
Replacement of exotic <i>Iris</i>	37
Limiting Factors	40
Light as a limiting factor	40
Vegetational strata (structure) as a limiting factor	43
Duration of water inundation as a limiting factor for <i>Iris</i>	47
Miscellaneous Observations	48
Evaluation of Methods for Abundance	49
Chapter 4	
DISCUSSION	51
<i>Lonicera japonica</i>	51
<i>Hedera helix</i>	57
<i>Iris pseudacorus</i>	64
Comparisons of the Three Exotic Species	71
Chapter 5	
CONCLUSIONS	75
TABLES	77
REFERENCES	167
APPENDIX I: STATISTICAL REFERENCES CONSULTED	171
APPENDIX II: SCIENTIFIC AND COMMON NAMES OF PLANTS	173
INDEX	175

# Photographs

Frontispiece	ii
Marsh and adjacent forest on Theodore Roosevelt Island	xvi
Quadrat frame (1 × 1m) in place on a plot of English ivy ( <i>Hedera helix</i> ) in an upland <i>Hedera</i> block.	6
Ozalid type light meter on the flood-plain free of exotics on north-east side of the island. Tall herb is <i>Impatiens capensis</i> .	6
Cheesecloth covered wire frames used for the controlled shade and light experiments with <i>Hedera helix</i> .	7
<i>Hedera helix</i> on the ground and climbing trees on the upland near the controlled shade and light experiments with this species.	33
The author (right) and his assistant, Michael J. Blymyer, working in an upland <i>Hedera helix</i> block.	50
Habitat of <i>Lonicera japonica</i> (Japanese honeysuckle) in a natural understory. Vine climbing a small tree.	74



# Figures

1	Theodore Roosevelt Island and vicinity.	2
2	Comparison of swamp-marsh transition <i>Iris pseudacorus</i> and <i>Peltandra virginica</i> by mean frequency/m <sup>2</sup> against time.	38
3	Comparison of open marsh <i>Iris pseudacorus</i> and <i>Peltandra virginica</i> by mean frequency/m <sup>2</sup> against time.	39
4	Comparison of <i>Iris pseudacorus</i> decline in swamp-marsh transition with that of the open marsh.	39
5	Comparison of <i>Peltandra virginica</i> increase in swamp-marsh transition with that of the open marsh.	40
6	Comparison of tree line stations with their bank stations in the marsh and swamp-marsh transition zone.	67

# Tables

1	Comparison of combined control plot frequency.	77
2	Comparison of dry weight biomass dominance.	78
3	Comparison of square decimeter grid frequency dominance.	79
4	Comparison of cover dominance of <i>Hedera helix</i> .	80
5	Comparison of growth over time of dry-weight biomass.	81
6	Comparison of 1 year dry-weight biomass growth.	82
7	Comparison of 1.25 years dry-weight biomass growth.	82
8	Comparison of growth over time by frequency in upland <i>H. helix</i> .	83
9	Comparison of growth over time by frequency in natural understory <i>L. japonica</i> from a randomized block design experiment.	83
10	Comparison of growth over time by frequency in natural understory <i>L. japonica</i> from a completely randomized design experiment.	84
11	Comparison of 1 year of growth with control by frequency in flood-plain <i>H. helix</i> .	84
12	Comparison of 1.25 years of growth with control by frequency in flood-plain <i>H. helix</i> .	85
13	Comparison of 1 year with 1.25 years of growth by frequency in flood-plain <i>H. helix</i> .	85
14	Comparison of 1 year of growth with control by frequency in cleared understory <i>L. japonica</i> .	86
15	Comparison of 90 days of growth with control by frequency in cleared understory <i>L. japonica</i> .	86
16	Comparison of 1 year with 90 days of growth by frequency in cleared understory <i>L. japonica</i> .	87
17	Comparison of 1 year of growth by frequency in two habitats each for <i>L. japonica</i> and <i>H. helix</i> .	87
18	Comparison of 1.25 years of growth by frequency in natural understory <i>L. japonica</i> and two habitats each of <i>H. helix</i> .	88
19	Comparison of growth over time by area covered in upland <i>H. helix</i> .	88
20	Comparison of growth over time by area covered in flood-plain <i>H. helix</i> .	89
21	Comparison of 1 year of cover growth in two habitats of <i>H. helix</i> .	90

22	Comparison of 1.25 years of cover growth in two habitats of <i>H. helix</i> .	90
23	Description of flood and its effects as a result of Hurricane Agnes.	91
24	Influence of <i>H. helix</i> and other ground cover on mud deposition.	92
25	Flood survival of <i>H. helix</i> on the flood-plain in frequency/m <sup>2</sup> .	92
26	Flood survival of <i>H. helix</i> on the flood-plain in square decimeters of cover/m <sup>2</sup> .	92
27	Flood survival of woody plants, herbaceous plants, and comparisons of woody and herbaceous plants on the flood-plain.	93
28	Comparison of herbaceous and woody plants in upland <i>H. helix</i> weeded (treated) and unweeded (control).	94
29	Comparison of herbs, trees, and other woody plants in upland <i>H. helix</i> habitat.	95
30	Comparison of herbaceous and woody plants in natural understory <i>L. japonica</i> weeded (treated) and unweeded (control).	96
31	Comparison of herbs, trees, and other woody plants in natural understory <i>L. japonica</i> habitat.	97
32	Comparison of <i>Podophyllum peltatum</i> L. in the upland forest in exotic ground cover weeded (treated) and unweeded (control).	98
33	Comparison of herbaceous and woody plants in flood-plain <i>H. helix</i> weeded (treated) and unweeded (control).	99
34	Comparison of herbs, trees, and other woody plants in flood-plain <i>H. helix</i> habitat.	100
35	Comparison of herbaceous and woody plants in cleared understory <i>L. japonica</i> weeded (treated) and unweeded (control).	101
36	Comparison of herbs, trees, and other woody plants in cleared understory <i>L. japonica</i> habitat.	103
37	Comparison of <i>Parthenocissus quinquefolia</i> in <i>L. japonica</i> natural and cleared understories.	104
38	Comparison of herbaceous plant increase in different habitats.	105
39	Comparison of woody plant increase in different habitats.	105
40	Comparison of tree increase in different habitats.	106
41	Comparison of woody plant (except trees) increase in different habitats.	106
42	Comparison of swamp-marsh transition, <i>I. pseudacorus</i> .	107
43	Comparison of swamp-marsh transition, <i>Peltandra virginica</i> .	108
44	Comparison of open marsh, <i>Iris pseudacorus</i> .	109
45	Comparison of open marsh, <i>Peltandra virginica</i> .	110
46	Comparison of <i>Iris pseudacorus</i> in swamp-marsh transition with that of open marsh.	111

47	Comparison of <i>Peltandra virginica</i> in swamp-marsh transition with that of open marsh.	112
48	Comparison of <i>Iris pseudacorus</i> and <i>Peltandra virginica</i> seed germination and survival.	113
49	The influence of <i>Acorus calamus</i> growth on <i>Iris pseudacorus</i> .	114
50	The influence of <i>Iris pseudacorus</i> growth on <i>Acorus calamus</i> .	114
51	Comparison of light by percent of open sunlight in forested habitats on 23 September, 1971.	115
52	Comparison of light by percent of open sunlight in forested habitats on 7 November, 1971.	116
53	Comparison of light by percent of open sunlight in forested habitats on 22 December, 1971.	117
54	Comparison of light by percent of open sunlight in forested habitats on 4 February, 1972.	118
55	Comparison of light by percent of open sunlight in forested habitats on 20 March, 1972.	119
56	Comparison of light by percent of open sunlight in forested habitats on 5 May, 1972.	120
57	Comparison of light by percent of open sunlight in forested habitats on 30 June, 1972.	121
58	Comparison of light by percent of open sunlight in forested habitats on 7 August, 1972.	122
59	Comparison of light by percent of open sunlight in marsh habitats on 7 November, 1971.	123
60	Comparison of light by percent of open sunlight in marsh habitats on 22 December, 1971.	124
61	Comparison of light by percent of open sunlight in marsh habitats on 4 February, 1972.	125
62	Comparison of light by percent of open sunlight in marsh habitats on 20 March, 1972.	126
63	Comparison of light by percent of open sunlight in marsh habitats on 5 May, 1972.	127
64	Comparison of light by percent of open sunlight in marsh habitats on 30 June, 1972.	128
65	Comparison of light by percent of open sunlight in marsh habitats on 7 August, 1972.	129
66	Comparison of light by percent of open sunlight in marsh habitats on 22 September, 1972.	130
67	Comparison of dry weight biomass for <i>L. japonica</i> .	131
68	Comparison of dry weight biomass for <i>H. helix</i> .	131
69	Comparison of chlorophyll for <i>H. helix</i> and <i>L. japonica</i> .	132
70	Comparison of dry weight <i>H. helix</i> leaf biomass.	133
71	Comparison of dry weight <i>L. japonica</i> leaf biomass.	133
72	Comparison of vigor of <i>H. helix</i> .	134

73	Comparison of vigor of <i>L. japonica</i> .	134
74	Controlled shade regression experiments on <i>H. helix</i> .	135
75	Controlled shade regression experiments on <i>L. japonica</i> .	138
76	Descriptive comparison of number of vegetational strata in different habitats.	141
77	Correlation of ground-layer heights in different but similar habitats.	142
78	The proportional number of strata present in each habitat.	143
79	Significant associations of one stratum with another.	144
80	Some associations of one woody stratum depth with another.	145
81	Discriminant function applied to differentiation of habitats with <i>H. helix</i> , <i>L. japonica</i> , and <i>I. pseudacorus</i> and similar habitats.	148
82	Relationship of living <i>Ulmus americana</i> overstory trees with <i>H. helix</i> and <i>L. japonica</i> .	149
83	Relationship of nonvigorous standing overstory trees ( <i>U. americana</i> and all others) to <i>H. helix</i> and <i>L. japonica</i> vines.	150
84	Tabular analysis of exotic vines with vigor and tree type.	151
85	Relationship of overstory-size down trees ( <i>U. americana</i> and all others) and type of fall (cut or natural) to <i>Hedera helix</i> and <i>Lonicera japonica</i> vines.	152
86	Percent of all down trees ( <i>Ulmus americana</i> and all others) with various types of <i>H. helix</i> and <i>L. japonica</i> infestation.	154
87	Tabular analysis of exotic vines with type of tree fall and tree type.	155
88	Tabular analysis of exotic vines with tree fall type and tree type.	156
89	Comparison of elevations in the open marsh and swamp-marsh transition zone.	158
90	Comparison of topographic elevations in the open marsh and swamp-marsh transition zone.	158
91	Comparison of dry-weight biomass with per cent of open sunlight and topographic elevation for <i>I. pseudacorus</i> .	159
92	Comparisons of presence or absence of <i>Peltandra virginica</i> in four microvegetation types.	160
93	Comparisons of soil color.	161
94	Comparisons of presence or absence of soil hardpan.	162
95	Comparison of total water discharge of the Potomac River.	163
96	Miscellaneous observations.	164
97	Comparison of three methods of determining dominance and rate of growth on <i>H. helix</i> , <i>I. pseudacorus</i> , and <i>L. japonica</i> .	165



# *Acknowledgments*

Many people have aided in the successful completion of this study. Special thanks are extended to Dr. W. D. Billings of Duke University Botany Department for his counsel in selecting this study problem as well as in research methods and procedures. Dr. Boyd Strain of the same department also provided advice on procedures. The statistical consultations with Dr. Roger Chapman of Duke University Forestry School were invaluable in facilitating the research.

The gathering of much of the data would have been impossible or exceedingly slow without field and laboratory help. The following temporary National Park Service personnel were hired at various times specifically to help me: Judith T. Simmons, Margaret E. Oliver, Michael J. Blymyer, and Mary T. Flynn. In addition, other people both in and out of the National Park Service provided or volunteered their help for which I am thankful. Special mention, because of his great assistance in placing and retrieving light meters, is due to William C. Wilkinson, III, who was site supervisor on Theodore Roosevelt Island.

The patience of my wife, Nancy, and my children during this project as well as their help is acknowledged gratefully. All except the youngest child has helped in the field or laboratory at some stage in the project and my daughter, Elizabeth, has helped several times.

LINDSEY KAY THOMAS, JR.  
*Duke University*



# Summary

Three exotic plant species were studied. *Lonicera japonica*, Thunb. (Japanese honeysuckle) and *Hedera helix*, L. (English ivy) are destroying the forests (except the swamp) of this low lying island in Washington, D.C. The marsh on this Potomac River island is being changed by *Iris pseudacorus*, L. (European yellow iris). Besides studying impact, limiting factors were also determined.

On the island upland *L. japonica* growth increases with light intensity. When shade is not a factor that limits this evergreen vine, it overwhelms and kills small trees and shrubs, and it inhibits reproduction, especially of the following trees which are among the overstory dominants on the upland of the island: *Ulmus americana*, L., *Prunus serotina*, Ehrh., and *Liriodendron tulipifera*, L.

On the upland there is no other factor that is stronger than light for limiting *H. helix* growth, but it is not as strong a limiting factor for this species as it is for *Lonicera*. On the flood plain, growth and distribution are limited by water table height. In both habitats, *Hedera* suppresses the growth of native herbs. This evergreen tendril liana climbs overstory and understory trees as well as small trees and is able to shade and kill them.

Marsh that would otherwise be occupied by *Peltandra virginica*, (L.) Schott & Endl. is taken over by *I. pseudacorus*. In the swamp-marsh transition *Acorus calamus*, L. takes over *Iris* areas. The length of time *Iris* is inundated by water comes closest to a factor limiting its growth. The shorter the inundation, the greater is the growth rate.



Marsh and adjacent forest on Theodore Roosevelt Island.

# *Introduction*

## *The General Problem*

One of the evidences of man's presence in an area is the occurrence of exotic plants. They may persist long after cultivation or other activities have ceased in the area, or they may escape husbandry and invade wild land. In either case, the exotic must have some impact upon the vegetation that is already present. Two objects cannot exist in the same spot at the same time. As a minimum impact, an exotic plant must displace an indigenous plant or occupy either a vacant habitat or niche. In either case, floristic composition of the vegetation and species absolute density have changed. The change may or may not be significant or have far-reaching ecological consequences. Although the situation is somewhat analogous to a foreign bacterium invading the human body, it is in fact a type of biological pollution of an ecosystem.

## *Location and Physical Description of Study Area*

Theodore Roosevelt Island, located at Washington, D.C., and administered by the National Park Service, U.S. Department of the Interior, was selected as a suitable area for studying the impact of exotic species because its human history and past land use are known, and it is a wild land area which contains exotic plant species some of which occur extensively there and elsewhere.

The island (Fig. 1) is located at a bend in the Potomac River and has a northwest-southeast axis (U.S. Geological Survey 1965). The 35.74-ha (88.32 acres) (National Capital Parks 1970:56) island is approximately 1.1 km (0.7 mile) long and 0.5 km (0.3 mile) wide at its widest place (U.S. Geological Survey 1965). The core of the island is micaceous schist surrounded by alluvium (Thomas 1963:1, 7). There are two topographically high areas on the island each about 13.1 m (43 ft) high (Thomas 1963:7). One high point is near the center of the island and the other is south of the center. The southwest side of the island generally slopes gradually to the alluvium, while the northeast side is generally steeper.



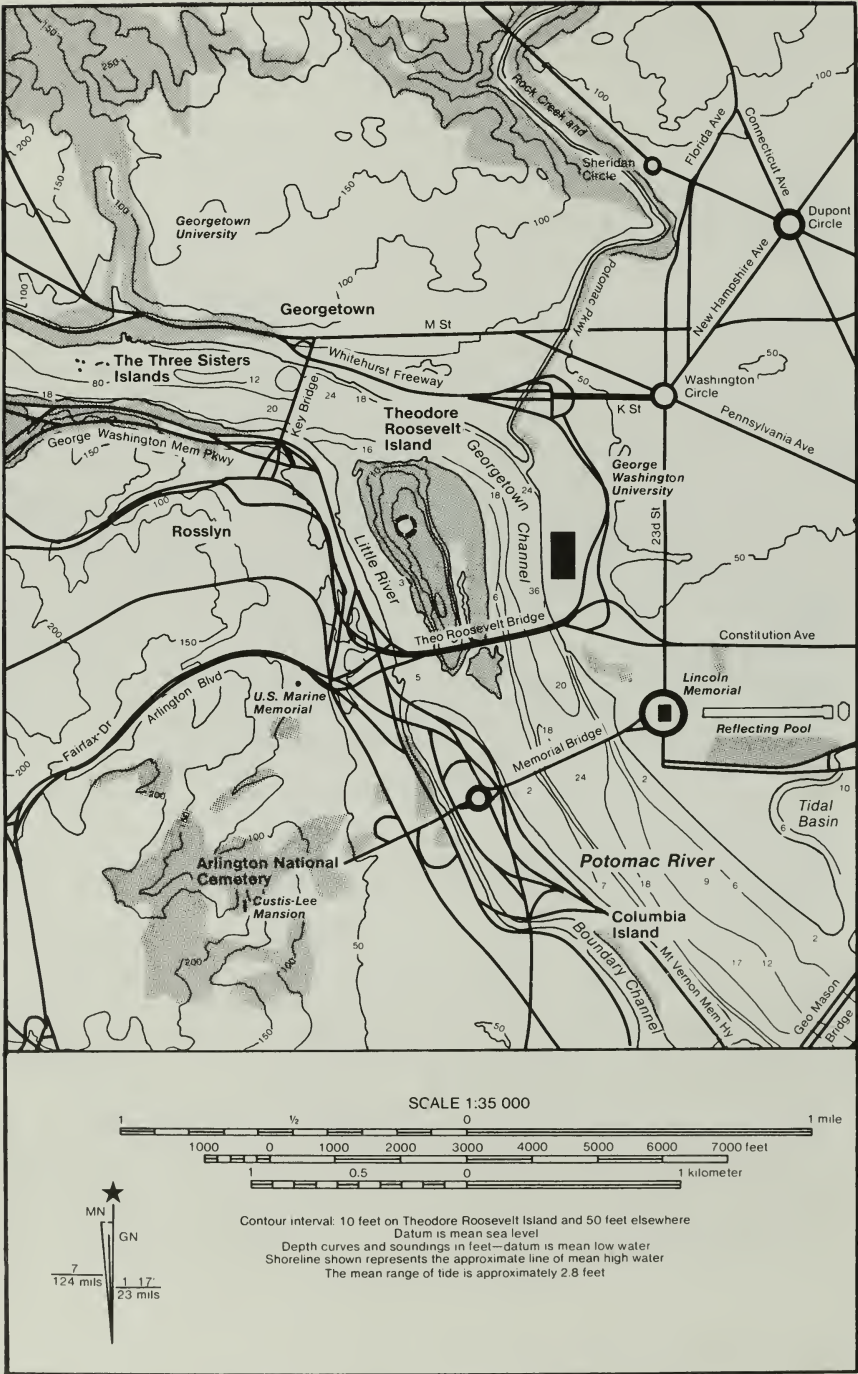


Fig. 1. Theodore Roosevelt Island and vicinity.

The alluvial deposits on the northeast side form a spit (Thomas 1963:7, 21-27, 47).

### *Summary of Human History and Past Land Use*

The island has had a varied history of human occupancy. The upland area was in agricultural use at least as early as 1792 by John Mason (Thomas 1963:2). The vegetation of the upland area has been disturbed periodically from that time until the island was acquired by the National Park Service in 1932 (Thomas 1963:2, 49). Aside from the construction of a highway bridge from 1959 to 1964 which passes over the southern end of the island, and a monument to Theodore Roosevelt which was constructed between 1963 and 1967 (Thomas 1963:2; U.S. National Park Service 1968:8), the last extensive vegetational disturbance took place between 1935 and 1937. This occurred mostly on the upland where 25 to 33 thousand trees and shrubs were planted (Thomas 1963:2, 49, 50). In preparation for this planting, brush, including Japanese honeysuckle (*Lonicera japonica*)<sup>1</sup> and some trees, particularly boxelder (*Acer negundo*), were removed. The flood of March 1936 apparently did extensive damage to many of these plantings (Thomas 1963:50).

### *Vegetation of the Study Area*

Unpublished notes and recollections which I made for an annotated floral check list for the island as well as for a dendrological survey indicate not only that most of the plantings did not survive but that the canopy trees are essentially the result of natural invasion in almost all areas of the island. The check list includes a number of exotic plant species some of which are the result of past plantings; some have apparently invaded the island from other locations. Some of these invading species are widespread over the island.

The dendrological survey indicates that the upland of the island is a mixed deciduous forest composed primarily of *Ulmus americana* (American elm), *Acer negundo*, *Morus alba* (white mulberry), *Prunus serotina* (black cherry), *Fraxinus americana* (white ash), *Liriodendron tulipifera* (tulip tree), *Quercus rubra* (northern red oak), and *A. saccharinum* (silver maple) in about that order. In the center of the upland area is a small grove of planted *Tsuga canadensis* (eastern hemlock) which does not appear to be reproducing (Thomas 1963:39, 52, 53). I noticed in 1971 and 1972 that the hemlocks apparently are dying out.

<sup>1</sup>Nomenclature of plant species follows that of Fernald (1950) unless otherwise noted.

The forested alluvial deposits are dominated by *Acer saccharinum*, *Fraxinus pennsylvanica* (green ash), and *Salix nigra* (black willow). Part of the alluvial forest is on hummocks which are not inundated in the annual floods; in this paper, this area is called "flood plain." Other parts of the alluvial forest occur in depressions and are inundated annually and sometimes daily by the tides; this area is called "swamp." *Taxodium distichum* (baldcypress) was planted in the 1930s (Thomas 1963:50).

The nonforested alluvial deposits are dominated by a freshwater tidal marsh. Some marsh occurs at various locations around the periphery but the largest marsh area occurs in the southeast part of the island between the upland and the spit (Thomas 1963:39). A gut or tidal creek flows south at ebb tide. The tide comes in usually twice a day, with a mean tidal range of approximately 0.9 m (2.8 ft) (National Ocean Survey 1971:228, Key Bridge, D.C.). I have observed that the marsh is not inundated every day by a high tide. The species which appear conspicuous by their abundance in the large marsh are *Peltandra virginica* (arrow arum), *Acorus calamus* (sweetflag), and *Typha angustifolia* (narrow-leaved cat-tail). Aspect dominance of *Iris pseudacorus* (European yellow iris, yellow flag) appears during its main flowering period of late May to early June. *Nuphar luteum* (L.) Sibth. & Sm. (Spatterdock) [*N. advena* (Ait.) Ait. f.] occurs extensively in the peripheral marshes.

Just north of the highway bridge, which is at the south end of the island, is a small grassy field.

### *The Species Selected for the Study*

Because of their abundance and apparent importance, three exotic plant species were selected for ecological study: *Hedera helix* (English ivy), *Lonicera japonica*, and *Iris pseudacorus*.

*Hedera helix* (Araliaceae) is an evergreen woody vine from Europe (Gleason 1952, 2:605). This ivy is widespread in the upland and flood-plain forests of the island, but there are some areas on the northeast slope that are free of the species. About 10 years ago, although English ivy was about as scattered as today, its main concentrations appeared to be around the Mason mansion site (topographic high point south of the central high point) and in the northwesterly section of the island. This ivy occurred on the island before the mass planting of the 1930s; in fact, it was recommended for preservation. Olmsted and Pope (1934: 7) say in their report:

But there are two plain evidences of former human occupation which are so agreeable in themselves and relatively so unassertive that they should be preserved rather than removed; namely the scattered areas of evergreen ground-cover of Periwinkle and English Ivy, the latter also climbing into some of the trees.

However unassertive it may have been in 1934, such was not the case by 1962 when I was collecting data for a plant check list. Today, an area of the southwest slope (northwest corner of the island), which 10 years ago was covered by *Claytonia virginica* (spring beauty), is now a dense ivy stand with few *C. virginica*. The meager evidence (concentration around the mansion site) suggests that English ivy was planted on the island when the Mason family lived there.

*Lonicera japonica* (Caprifoliaceae) is an evergreen woody vine from east Asia (Gleason 1952, 3:297). This species, like English ivy, is widespread in the upland and flood-plain forests of the island and absent on some sections of the northeast slope. Most of the honeysuckle stands do not appear to be as dense as the English ivy stands. One noticeable exception is south of the Mason house site and just northwest of the grassy field. This is an area where National Park Service maintenance crews removed the underbrush. Honeysuckle does not appear to be as abundant as 10 years ago. Areas that were formerly honeysuckle now seem to be mostly English ivy. The northwest part of the island appears to be such a case. Like the ivy, honeysuckle was here before the mass planting of the 1930s (Olmsted and Pope 1934:7, 8). Honeysuckle seems to invade when the vegetation becomes disturbed (Thomas 1963:50). No Japanese honeysuckle occurred in 1935 on the small island (Little Island) just downstream from Theodore Roosevelt Island, but a dense stand of *Acer negundo* existed. The boxelders were removed apparently the same year, and by 1962 Little Island was heavily covered by honeysuckle and English ivy occurred there at least by 1962. The southern end of the flood plain of this small island is presently covered with the ivy.

Japanese honeysuckle is abundant in wild lands near Washington, D.C., other than Theodore Roosevelt Island. This is not as true of English ivy.

*Iris pseudacorus* (Iridaceae) is a perennial herb from Europe (Gleason 1952, 1:446) that grows in marshes. On the island, this species is scattered primarily through the araceous zone of the marshes. This zone is dominated by *Peltandra virginica* and *Acorus calamus*. This exotic species was also on the island before the mass planting of the 1930s (Olmsted and Pope 1934:9). Although the iris appears to be abundant in the large marsh on the island, it does not seem as abundant in nearby marshes of the Potomac and Anacostia rivers.

### *The Purpose of the Study*

Answers to three questions were sought for these selected exotic species. How important are these exotics in the habitats in which they are abundant? What native and exotic species or life forms, if any,



replace each other? What factors limit the degree of exotic abundance?

By studying the abundance of a given exotic in more than one habitat, the susceptibility of different vegetations to that exotic can be learned, and by studying the same habitat both with and without the exotic, the possible transformation or change from one vegetation to another can be assessed. Floristic and vegetational changes and limiting factors give information on the dynamics of exotic species impact. Limiting factors also give information which is valuable for managing and controlling the invading weed.



Quadrat frame ( $1 \times 1\text{m}$ ) in place on a plot of English ivy (*Hedera helix*) in an upland *Hedera* block.



Ozalid type light meter on the flood plain free of exotics on northeast side of the island. Tall herb is *Impatiens capensis*.



## *Materials and Methods*

### *Design of Observations and Statistics*

Survey designs used were census, simple or complete random sampling, paired plots, and model II regression. The experimental designs used in this study were complete randomization (for both two and more groups), paired plots, randomized complete block, Latin square, and model I regression. Except in a very few obvious instances, all data (both discrete and continuous variables) were statistically analyzed. Because statistical analysis of samples is based on homogeneous variance, this was tested either by Bartlett's test or variance ratio test (and in many cases brought into homogeneity by a transformation) before the  $t$  test, analysis of variance, analysis of covariance, regression, or chi-square test was applied. The only arc sine transformations made in my study are in degrees not radians. If the variance remained heterogeneous, then a modified  $t$  test or other statistical test of comparison was applied. If the variance was on the borderline (usually 0.1 or 0.05), the statistical test of comparison was used both modified and unmodified. The  $t$  tests



Cheesecloth covered wire frames used for the controlled shade and light experiments with *Hedera helix*.

were modified by methods given both by Snedecor and Satterthwaite. For a modified paired  $t$  test, the samples were unpaired and considered as equal sample sizes. Modification for a one-way analysis of variance was to set the significance level higher at 0.05 and rely more on the biology, or at 0.005 and rely more on physical conditions. A significant heterogeneity chi-square required reliance on the individual chi-squares. With every analysis of variance or covariance, Duncan's "new multiple range test" was applied when replications were equal, and Kramer's modification was applied when replications were unequal or variances were heterogeneous, or means were correlated. (In the tables, both tests are referred to as Duncan's test.)

Whenever a regression was applied, it was tested for significance and the coefficient of determination (or multiple determination) computed.

Significance levels were set as follows. Because of the variation in biological material in the field, significance levels were set for field experiments as well as surveys at 0.1 (10%). Physical material was expected to vary less; therefore, when only these were involved, significance was set at the 0.01 (1%) level. (One exception was made when published data were analyzed.) For experiments using biological material isolated from its usual surroundings and over which more control could be exercised, the significance level was set at 0.05 (5%). All experiments were replicated at least three times and all surveys were based on at least three replications of the sample unit.

Most of the field experiments and all of the sample survey units were set up at random on the island by use of a random digits table. I consistently used the method described by Phillips (1959:23) for locating starting digits in the table.

The statistical references consulted are listed in the Appendix.

### *The Physical Setup (Materials)*

#### **The Habitats Studied**

To answer the questions on exotic impact a well-integrated physical setup was needed since many of the experiments and surveys were performed on a given set of quadrats or points. This will be described and the experimental and survey observational methods related to it.

Each of the three exotic species was studied in two different habitats. *Hedera helix* was studied on the upland and in the flood plain. *Lonicera japonica* was studied in an area where the forest understories were intact and in an area where the underbrush had been removed several years ago by the National Park Service; both are on the upland. *Iris pseudacorus* was studied near the tidal gut and by the tree line (edge of the swamp); both of these areas are in the big marsh.

## The Placement of $1 \times 1$ -m Quadrats

After an inventory of all the possible areas, ten blocks of three  $1 \times 1$ -m quadrats each were laid out at random on the upland in *Hedera helix*. The  $1\text{-m}^2$  plots in each block were laid out 0.5 m apart on the contour by using a tape, surveyor's rod, and level. To assure each block being a valid replication of the others, uniformity of coverage by the exotic was set as close to 100% as possible. This principle applies to all randomized block and paired plot designs. Plots containing much less than complete coverage by the exotic could be used, in theory, but would be hard to replicate. One plot in each block was a control that received no treatment, whereas the other two did. The selection of plots for treatment or controls was by a random digits table; this principle applies to all selection of control and treatment plots. The treatments will be described later. There were, then, 30,  $1\text{-m}^2$  quadrats, 20 of which received a treatment.

On the flood plain, seven blocks of three  $1 \times 1$ -m quadrats each were laid out in *Hedera helix* plus a placement of one pair of  $1 \times 1$ -m plots (one of which was a control plot). This gave 8 control plots and 15 treated ones. For some studies, more were needed and an additional five  $1 \times 1$ -m plots were randomly selected. On the flood plain (a flat area), the three plots within each block were laid out on the corners of an equilateral triangle. A minimum of 0.5 m separated the plots at their closest points; this same separation held for the pair. The reason for this mix of designs was the physical impossibility of placing any more complete blocks or pairs in otherwise suitable *H. helix*; there were too many trees and shrubs in the way. For this area, then, there were 28,  $1\text{-m}^2$  quadrats.

The placement of plots ( $1 \times 1$  m) in *Lonicera japonica* under a natural understory presented problems similar to those encountered on the flood plain with *Hedera helix*. Although *L. japonica* is widespread and abundant, finding areas large enough to place two or three quadrats and have all quadrats be uniformly covered (for valid replication) with the exotic is a problem. For *L. japonica* under a natural understory, three blocks of three  $1 \times 1$ -m plots each were placed. They were laid on the contour as described for *H. helix* on the upland. An additional five pairs were also laid out on the contour, thus making a total of 19,  $1\text{-m}^2$  plots, 8 of which were controls and 11 received treatment.

When only two plots of a randomized block layout were used, they were used as paired plots. Whenever possible in the case of mixed designs, analysis was run two ways as a means of verification. For example, part of the data analyzed by randomized block with three replications could be analyzed by paired plot. Eight paired plots (three from the block design and five pairs as originally set up) were used to verify an aspect of the block design.

Ten pairs of  $1 \times 1$ -m quadrats were placed at random and on the

contour in the *Lonicera japonica*, which is in the forest area cleared of underbrush. One plot of each pair was randomly selected as a control plot. These also were 0.5 m apart in the pairs.

In the marsh, both near the gut and near the swamp forest edge, some latitude had to be allowed regarding distance between plots within a block or a pair, because in many places, particularly near the gut, *Iris pseudacorus* grows in clumps often about 1 m<sup>2</sup> in area. Thus, the plots were often further apart than 0.5 m. In all cases where blocks could be laid out, the plots formed a triangle but not necessarily equilateral. The orientation of each plot was governed by where the *Iris* was or was not.

In the marsh toward the gut, I laid out all the blocks of three 1 × 1-m plots and paired 1 × 1-m plots that were possible. This resulted in three blocks of three plots each and four pairs of plots. This provided seven control plots and ten plots for treatment. An additional five 1 × 1-m plots were randomly selected, thus giving a total of 22, 1-m<sup>2</sup> plots for this area.

For the marsh area near the swamp forest line (swamp-marsh transition), I also laid out all the blocks of three plots and all the pairs possible. This resulted in four blocks of three 1 × 1-m plots each and nine pairs of 1 × 1-m plots. This provided 13 control plots and 17 plots for treatment. An additional three 1 × 1-m plots were randomly selected thus giving a total of 33 plots in this area.

Altogether, 152, 1 × 1-m plots were placed in blocks, pairs, or singly in six habitats involving three exotic species and satisfying the randomization needed for statistical analysis. In the forested areas, the corners of the 1 × 1-m plots were marked by nails or spikes about 15 cm long, tied with white cord and driven into the ground. In the marsh these are too short because they tend to sink into the mud too readily. To mark the corners of the marsh plots, spikes 26 cm long and tied with colored surveyor's flagging were used. Around the blocks and paired plots, a simple fence of string with surveyor's colored flagging tied on it was placed to remind park visitors not to walk on the plots. Wooden stakes (2 × 2 inch—or more like 4 × 4 cm) were used as fence posts; sometimes trees were used.

### The Placement of Light Stations

An extensive layout of light stations was set up on the island to test the hypothesis that light is a limiting factor in the spread and growth of these three exotic species. To accomplish this, 126 light stations were set up in the following areas for the purposes stated. A light station was established for each block and paired plot. For the blocks that occurred three in a row on the contour, a random digits table was used to determine whether the station should be placed between plots 1 and 2 or between 2 and 3. For blocks with the plots placed on the corners of a triangular



area, the station was placed in the middle of the triangle and surrounded by the three plots. Stations were established between paired plots.

Comparisons were made in similar habitats without the exotics. Ten stations were placed at random in the upland forest where exotics were not noticeable and *Hedera helix* and *Lonicera japonica* were absent. Another 10 were placed similarly at random on the flood plain. Twenty stations were randomly placed in the marsh where there were no *Iris*. Ten of these were in the open area and ten in the swamp-marsh transition near and at the tree line. The random placement of these 40 light stations in areas of nonexotic vegetation was accomplished by drawing coordinates at random (from a random digits table) for a grid placed on a map of the island. Because each division of the grid was about 2.3 m, no backsights and only one foresight was taken in the field in locating the points on the ground. This was done to ensure error and hence increase randomization.

All light measurements were compared with open sunlight. For this purpose, 10 randomly placed stations were located in the open field just north of the highway bridge. Coordinates of a grid were placed on the ground in the open area and random coordinates selected by means of a random digits table.

There was some concern that the lights from the highway bridge might influence the light readings. To check this, an additional 20 stations were placed randomly (by using a random digits table) along the four stone railings of the two bridges at the monument to Theodore Roosevelt, which is just north of the center of the island. These bridges are at the northwest and southeast sides of the monument area.

The light meters (Ozalid type) in the forest areas were placed at the height of the vegetation layer beneath the shrub layer at that point; nails, spikes, or metal rods were used to support the meters. Masking tape was used to fasten the meters to the support except where the meter was on the ground; in such cases, three nails driven into the ground around the meter held it in place. In the marsh area and the field, the meters were placed at the height of the tall herb vegetation at that point. Masking tape was used to fasten them to the wooden support stakes. A grease pencil was used to mark the stations on the stone rails of the monument. Because masking tape does not stick well to a wet or damp stone surface, filament tape was placed on the stone when dry and masking tape was used to fasten the meters to the filament tape surface.

To mark the location of the forest light stations and to be able to find them with snow on the ground, if need be, a cord was fastened from the support to some nearby vegetation and a colored ribbon of surveyor's flagging was tied to the cord.

The Ozalid meters are sensitive to wavelengths around 410  $m\mu$  (Friend 1961:579).

## The Placement of Vegetational Strata Stations

Another means of investigating light was to study the stratification of vegetation in areas where trees and shrubs were present. With the exception of the points on the monument, in the field, and in the marsh away from the swamp-marsh transition zone, the light stations doubled as sampling stations for investigating stratal relationships. In addition, 13 points were established in the swamp in the following manner. A line was laid perpendicular to the tree line closest to the light station in an *Iris* block or paired plot in the swamp-marsh transition area. This perpendicular line not only passed through the station but also extended to a point away from the marsh and passed obvious *Iris* until about halfway under the first limb of the first canopy tree. These points were marked with flagged stakes.

## The Placement of Elevation Stations

To provide a description of the flood crest, five elevation stations were selected, but not at random. The selection was based on access during the flood as well as a representative sample. In relation to the upland (not flood plain) part of the island, the points were located as follows: northeast, north-northeast, north, west, and southwest. Two other stations were marked, but they disappeared.

The 20 light stations in the marsh not associated with plots plus the centers of the 20 control plots in the marsh were used as elevation stations in relation to investigating water as a limiting factor. In addition, 10 more elevation stations were located on the bank of the tidal gut closest to the non-*Iris* swamp-marsh transition zone light stations.

## The Competition Experiments

Twenty-five wire baskets, 10 cm high, about 22 cm in diameter, and lined with treated paper (for water retention), were placed on a sloping metal roof which is shielded on two sides. These baskets were placed in the form of a square with five baskets on a side and were used in a  $5 \times 5$  Latin square experimental design in an *Iris* competition study. Holes cut in thin plywood held the baskets about 25 cm apart; C-clamps held the plywood to the roof.

## The Germination Observations

Twenty-five cans 17.5 cm high and 10.5 cm in diameter were used for germinating seeds. These were placed in the form of a square and attached to the same roof in the same manner. The center of each can was 30 cm from its neighbor.



## The Controlled Shade and Light Experiments

Two sets of experiments with sunlight and degrees of shading were performed: one in a dense stand of *Hedera helix*, the other in a dense stand of *Lonicera japonica*. The physical layout for each was as a randomized complete block experiment with a control, and four treatments each of which were replicated 3 times. Each block of five  $1 \times 1$ -dm plots was placed on the contour. Two nails about 15 cm long marked the location of the uppermost corners of each plot. Each plot was covered by a wire basket about 22 cm in diameter and 31 cm high. Prongs on the bottom of the baskets about 5 cm long were pressed into the ground to help hold the baskets in place. Except for the controls, the baskets were wrapped in layers of cheesecloth: 12 layers, 24 layers, 48 layers, and 96 layers. When light measurements were taken, the meters, attached to 15-cm nails with masking tape, were placed in the center of each 1-dm<sup>2</sup> plot. Altogether there were 30 plots each 1 dm<sup>2</sup>.

## The Censuses

A census was taken for the three surveys involving *Ulmus americana* and exotic vines. The total trees involved were 1132.

## The Observational Methods

### Control Check

All control plots were read for exotic frequency in the spring of 1972 (the observed frequency) and compared with the reading of the same plot in the spring of 1971 (the expected frequency) by a chi-square analysis of  $1 \times 2$  tables. The reading dates were as follows: upland *Hedera*, 31 March; natural understory *Lonicera*, 1 April; flood plain *Hedera*, 1–5 April; open marsh *Iris*, 2–4 April; swamp-marsh transition *Iris*, 2–5 April; cleared understory *Lonicera*, 12 and 13 April. With the exception of the open marsh *Iris*, the analysis was on the pooled data for all the control plots. The exception, due to heterogeneity (significant beyond 0.001), required analysis of the individual chi-squares for each of the seven control plots. The results are shown in Table 1 (following Chapter 5). By May 1972, when the plots were read and biomass would have been collected, it was patently evident that the *I. pseudacorus* plants were dying out in the transition area as well as in the open marsh.

The control plots for upland and flood-plain *Hedera* were also read for cover to the nearest 0.5 dm<sup>2</sup> at the same time that frequency readings were taken. In 1971, the mean of 10 upland plots was 99.4 dm<sup>2</sup>/m<sup>2</sup> of *H. helix*, while in 1972 the mean was 99.6 dm<sup>2</sup>/m<sup>2</sup>. For the flood plain,

the mean of eight plots in 1971 was  $98.5 \text{ dm}^2/\text{m}^2$ , and in 1972 it was  $98.6 \text{ dm}^2/\text{m}^2$ . In each case (upland and flood plain),  $t$  tests showed no significant differences at 0.1 between the two dates. Since cover data are available only for *Hedera* and these data support the frequency for the same species, and since it appeared desirable to treat all species alike as much as possible, frequency was the characteristic counted, tested, and then presented in Table 1.

### Importance of the Exotics in Different Habitats

To answer the question of how important these three exotic species are in the habitats in which they are abundant, the ecological dominance and growth rate were determined for each species in each of two habitats. In addition, the flood from Hurricane Agnes (June 1972) changed some study plans but made it possible to study the importance of *Hedera helix* on the flood plain under more severe conditions.

*Ecological Dominance.* Dominance was determined by three methods: biomass, frequency, and cover.

1. Biomass. One very good way to determine dominance in non-arborescent vegetation is to measure the biomass of each species. A biomass survey by simple random sampling of  $1 \times 1\text{-m}$  quadrat plots was made of the three exotics in each of two habitats, six habitats in all. All the *Lonicera japonica* were collected from the 11 treatment plots in the natural understory area 9 and 10 April 1971 and from the 10 treatment plots in the cleared understory area 13, 14, and 15 April 1971. All the *H. helix* were collected from the 20 upland treatment plots 16–22 April 1971, and from the 15 treatment and 5 extra single plots on the flood plain 22–29 April 1971. All the *Iris pseudacorus* were collected from the 17 swamp-marsh transition treatment plots and the 3 extra single plots 3–15 May 1971, and from the 10 open marsh treatment plots plus the extra 5 single plots 10–18 June 1971. In all cases, a wooden frame,  $1 \times 1 \text{ m}$  inside measurement, was placed on the plot and a sharpened sidewalk scraper cut around the perimeter to a depth of about 15.2 cm. As many of the roots as possible were taken to approach maximum accuracy.

Except for the *Iris pseudacorus*, the plant biomass of the weedy species was placed in paper bags by plot. The *Iris* required a different treatment because the soil could not be easily shaken off as was the case with *Lonicera* and *Hedera*. To facilitate the washing of *Iris* in water, the leaves and aerial stems were separated from the rhizomes. After washing, the *I. pseudacorus* was air-dried in the laboratory so it would keep until biomass determinations could be made. The temperature of several of the rooms in the laboratory was raised to 38–50° C to facilitate

this, and fans helped to move the air. When the material felt dry, it was placed in paper bags by plot.

The biomass was oven-dried at  $67 \pm 2^\circ \text{C}$  for 48 hours. Immediately after drying, weighing began on a quadruple beam balance that weighs to 0.01 g. The data were then rounded to the nearest whole gram per plot for *Hedera* and *Lonicera* and the nearest 5 g per plot for *Iris*.

The variances were heterogeneous; therefore, the one-way analysis of variance on the completely randomized samples was modified. In addition, *t* tests were computed on some of the data for further clarification.

After the biomass determinations were made, the dried material was returned to the plots from which it came. The dried material acted as a mulch to keep the soil from drying out; this function was performed by the living material in the control plots.

2. Frequency. Biomass determinations are time-consuming. Frequency (presence or absence) is obtained quickly. Dominance on a frequency basis was studied to determine whether it might be obtained and analyzed like continuous or measurement variable data in future investigations. Before the biomass was removed from the above plots, the plots were read for frequency of the exotic under study. In addition, all the control plots were also read; thus there were 152,  $1 \times 1$ -m plots for frequency determinations. The 19 *Lonicera japonica* plots under a natural understory were read 31 March and 1 April 1971. The 20 *L. japonica* plots under a cleared understory were read 12 and 13 April 1971. The 30 *Hedera helix* plots on the upland were read on 31 March 1971. The 28 *H. helix* plots on the flood plain were read 1, 2, 5, 22, and 23 April 1971. The 33 plots of *Iris pseudacorus* in the swamp-marsh transition area and the 22 *I. pseudacorus* plots in the marsh toward the gut were read 2, 3, and 5 April 1971.

Each plot was read in the following manner. The aforementioned meter-square quadrat frame was equipped with string to make a grid divided into  $1 \times 1$  dm. The 100-dm<sup>2</sup> grid was laid on each plot and the presence of the exotic under study tallied when it occurred in any degree within one of the  $1 \times 1$ -dm divisions. With *I. pseudacorus*, some probing into the surface mud was necessary to make this determination.

Because the variances of these six groups were heterogeneous on both the original frequency data and the arc sine transformed data, the one-way analysis of variance on the completely randomized samples was modified as described earlier.

3. Cover. A third test for dominance was to measure cover in square decimeters. In time consumption, this is intermediate between frequency and biomass determinations. Cover determinations were practical only with *Hedera helix* with its relatively broader leaves. On the same day frequency was counted, the aforementioned 100-dm<sup>2</sup> grid was used to

estimate cover to the nearest 0.5 dm<sup>2</sup> for the 30 upland and 28 flood-plain *H. helix* plots as previously described. Because the variances were heterogeneous for the two groups, a modified *t* test for unpaired plots and unequal replications was used in comparing the means.

*Growth Rate.* Growth rate was determined three ways on plots set up for randomized complete block and paired plot experimental designs only: biomass, frequency, and cover. Because the *Iris* was dying out, growth rates were studied only on *H. helix* and *Lonicera japonica*. Frequency and cover were recorded on the same day that biomass was removed for the second time from each plot. Frequency was to be analyzed by continuous or measurement variable statistics.

1. Biomass. For the growth rate on a biomass basis, one of the two treatment plots in every block of three plots was weeded of the exotic under study 1 year after the first removal. The exotic biomass was removed from the other treatment plot 1.25 years after the first biomass removal. The choice of which plot was to receive the annual weeding was made by a random digits table. In the case of the paired plots associated with the flood-plain *Hedera* and *Lonicera* under a natural understory, biomass was removed from the treatment plots at 1.25 years of growth. With the paired *Lonicera* plots under a cleared understory, biomass was removed from the treatment plots 1 year after the first weeding, and then again 90 days later. Biomass was removed, dried, and weighed as previously described. Three biomass growth-rate experiments each comparing 1 year and 1.25 years were analyzed as follows. Because the variance ratio test for the upland *Hedera* showed heterogeneity at the 0.1 level but not the 0.05 level, the paired plot *t* test was performed for data analysis in both the usual manner and with modification. The natural understory *Lonicera* was analyzed by a *t* test for unpaired plots. Data for the flood-plain *Hedera* experiment were analyzed in the same manner as the natural understory *Lonicera*. Analysis of the cleared understory *Lonicera*, comparing 1 year with 90 days, required the modified paired *t* test.

A fifth experiment compared the annual biomass of the two *Hedera* and two *Lonicera* areas, and a sixth experiment compared the 1.25 years' biomass of the two *Hedera* areas and the natural understory *Lonicera* area. A modified one-way analysis of variance for a completely randomized design, as previously described, was used in the data analysis of each experiment. In addition, both modified and unmodified *t* tests were computed for some of the data for further elucidation.

2. Frequency. Although growth rate on a frequency basis was more quickly obtained than collection of biomass, the statistical analysis took longer. In addition to using the same plots for frequency as were used for biomass growth rate, the associated control plots were also used. Where analysis of variance or *t* tests were used, both the original fre-



quency data and the arc sine transformed data were analyzed. Because the frequency tally for the annual growth was taken at a different time than for the 1.25 years or 90 days of growth, the control plots themselves had to be analyzed to make sure that they had not changed between the two readings. This meant comparing the control with itself as a paired plot in time. For the upland *Hedera* and cleared understory *Lonicera*, no change at all took place in the controls, so no statistical test was needed. For the natural understory *Lonicera*, the paired *t* test showed no significant change at the 0.1-level whether three paired replications (blocks only) or eight paired replications (blocks and paired plots) were used. (Eight pairs on original data required a modified as well as unmodified paired *t* test.) A modified paired *t* test of the controls in the flood-plain *Hedera* for seven pairs showed a significant change at the 0.05-level for original data and at the 0.02-level for transformed (arc sine) data. The change was a decrease in *Hedera* at the 1.25 years' reading which took place after the flood from Hurricane Agnes. Chi-square tests set up in  $1 \times 2$  tables for both seven and eight control plots and comparing expected frequency (at the annual reading) with observed frequency (at the 1.25 years' reading) showed heterogeneous data. In both cases, five plots showed a significant change (decrease) in *Hedera*, thus verifying the previous tests. This meant that the control, annual, and 1.25 years' readings could not be compared simultaneously in a randomized block of seven replications.

The statistical analysis of the upland *Hedera* was a modified analysis of variance for a randomized complete block experimental design. In this case, transformation (arc sine, square root, and logarithmic) did not bring homogeneity to the variances and the modification was to rely on the biology. As a check on this analysis, a modified paired *t* test on original data and unmodified paired *t* test on arc sine transformed data were run on the 1 year's and 1.25 years' frequency.

The growth rate by frequency for natural understory *Lonicera* was analyzed by analysis of variance for the randomized block experimental design with three replications, then the combined randomized block and paired plots were analyzed by modified one-way analysis of variance for both arc sine transformed data and original data.

The frequency data for flood-plain *Hedera* growth rate were analyzed by a modified paired *t* test (seven pairs) and by examination of individual chi-squares for each plot pair of the April control readings and annual growth. Another experiment compared the July control readings with 1.25 years of growth with a paired *t* test (eight pairs) and by analyzing the individual plot-pair chi-squares. A third experiment compared the annual and 1.25 years of growth by a paired plot *t* test (seven pairs) as well as individual chi-squares for the plot pairs.

Growth rate by frequency in the cleared understory *Lonicera* was also investigated by three experiments and analyzed by *t* tests and chi-

square tests as follows: control and annual growth as well as control and 90 days of growth, modified paired  $t$  and pooled chi-square; annual and 90 days of growth, modified and unmodified paired  $t$  and evaluation of individual chi-squares.

Another experiment compared the annual growth of the two *Hedera* and two *Lonicera* areas by a modified one-way analysis of variance on a completely randomized design.

The same experimental design was used in studying the 1.25 years of growth of *Hedera* and *Lonicera*. The original frequency data were analyzed by a modified one-way analysis of variance, but the transformed data required no modification of that statistical test.

3. Cover. A third way of studying growth rate was by investigating cover ( $\text{dm}^2/\text{m}^2$ ) in plots containing annual and 1.25 years of growth as well as control plots. This was applicable only to *Hedera* areas. The controls were checked against themselves for significant change in time, both from 1971 to 1972 as well as the dates in 1972 because annual and 1.25 years' cover was estimated (as previously described) on different dates. The paired  $t$  test, modified and unmodified as the situation required, was used in analysis of the controls.

There was no significant change in the upland *Hedera* controls, but the analysis of variance on a randomized block design had to be modified (as previously described) because no transformation tried (arc sine, square root, logarithmic) resulted in a homogeneous variance. For this reason also, modified paired  $t$  tests were used to compare the controls with 1 year of growth and the controls with 1.25 years of growth; an unmodified paired  $t$  test was used to compare annual and 1.25 years of growth on a cover basis.

The controls of the flood-plain *Hedera* did change significantly (beyond the 0.001 level) after the flood of Hurricane Agnes; therefore, three paired plot experiments were conducted. The controls compared with 1 year of growth as well as the controls compared with 1.25 years of growth required modified  $t$  tests. Modified and unmodified  $t$  tests were used to compare the 1 year with the 1.25 years of growth.

Unpaired  $t$  tests were used to compare 1 year of growth of upland *Hedera* with 1 year of growth of flood-plain *Hedera*, and 1.25 years of growth in the same two habitats.

*Importance on the Flood Plain.* The importance of *Hedera* on the flood plain was investigated not only as to how well it survives floods but also as to its influence on sediment deposition.

1. Flood Description. The flood resulting from Hurricane Agnes provided conditions which allowed assessment of the importance of *H. helix* on the flood plain. The height of the crest which occurred 24 June 1972, at Theodore Roosevelt Island was determined from an average of



five stations. The elevations at these five nonrandom stations were determined by a surveying altimeter. Datum is mean sea level. In spite of the nonrandom selection of points, confidence limits at the 10% level were calculated and the crest range determined.

The mean depth of mud with confidence limits and the range of mud depth deposited on the island were determined in centimeters. The depth was measured 25–28 July 1972 (about one month after the flood crest) in the center of each of the 23-m<sup>2</sup> flood-plain *Hedera* plots and at each light station associated with these plots (total of 31 sampling points).

2. **Mud Deposition.** This experiment to determine whether the presence or absence of *Hedera* and other ground cover influenced the depth of mud deposition was done before the survey to determine average mud deposition. The experiment compared the flood-plain *Hedera* control plots with the plots which had been weeded of *Hedera* at two different times. (One set of plots had not been weeded since April 1971 and the other set had been weeded April 1972.) The comparison of the plots was made by an analysis of variance for the randomized complete block design utilizing the seven blocks.

3. **Survival of Plants.** Three groups of surveys were carried out to determine what species or group of plants best survived the flood of Hurricane Agnes: *Hedera* as determined by frequency, *Hedera* as determined by cover, and other woody and herbaceous plants as determined by number per square meter. These surveys were all done on the control plots of the flood-plain *Hedera*. Frequency and cover (in dm<sup>2</sup>/m<sup>2</sup>) were determined as previously described, but frequency was analyzed by methods for discrete variables.

Frequency of *Hedera* survival was analyzed by considering the chi-squares of the individual plots which were analyzed in  $1 \times 2$  tables, since the heterogeneity chi-square was significant beyond the 0.001 level. In these tables, the observed frequency (25–28 July 1972) about 1 month after the flood was compared with the expected frequency (26–29 April 1972) before the flood.

A modified paired *t* test (seven pairs) was used to analyze the cover data for flood-plain *Hedera*.

Determination of cover for other woody plants and herbaceous plants would not be as accurate because of the different growth forms. Such plants were counted and the data square root transformed ( $\sqrt{x + 0.5}$ ) before analysis by *t* tests (modified and unmodified) for paired plots (seven pairs).

The following comparisons of before and after the flood were made: all woody species collectively, all herbaceous species collectively, and a comparison of herb and woody plant survival. For this latter comparison, the differences from the data for paired plots for herb survival were compared (paired *t* test) with the differences from the data for

paired plots for woody plant survival. In addition, *Acer negundo*, a common tree species, and *Lindera benzoin* (spice bush), a common shrub species, were investigated for flood survival.

The assessment or rating of flood survival for these groups and species is based on degree or level of statistical significance.

### Replacement of One Species or Life Form by Another

The second major question, life form and species replacement, is divided into two problems: what has the exotic *Hedera* and *Lonicera* replaced, and what is replacing the exotic *Iris*.

*Replacement of Native Life Forms and Species.* To solve the first of these problems, 41 experiments were performed to determine what would grow on 1-m<sup>2</sup> plots from which the exotic plants had been removed. The general plan was to study each of the four habitats (two *Hedera* and two *Lonicera* habitats) separately and then to compare the habitats. In each habitat, the herbs were counted in both the control plots and the plots weeded for annual biomass growth and compared by a paired *t* test. The same was done for woody plants except that the counts were made from plots weeded for 1.25 years of growth rather than for annual growth. In the *L. japonica* area with the cleared understory, the herb and woody plant counts were made on the same treated plots as well as the control plots. There were enough woody plants to allow a further breakdown into trees and other (shrubs, ferns, woody vines); these also were analyzed by a paired plot *t* test. In the flood-plain *Hedera*, the herbs could be divided into annual (entirely *Impatiens capensis* (spotted touch-me-not)) and other (biennial and perennial). These were each analyzed by paired plot *t* tests. In a number of other instances, individual species were abundant enough for individual analysis by a paired plot *t* test: *Prunus serotina* and *Parthenocissus quinquefolia* (Virginia creeper) in the natural understory *Lonicera* area, and *Allium vineale* (field garlic), *Oxalis stricta* (wood sorrel), *Liriodendron tulipifera*, *Ulmus americana*, *P. quinquefolia*, *Rhus radicans* (poison ivy), and *Vitis rupestris* (sand grape) in the cleared understory *Lonicera* habitat.

For each of the four habitats, the invasion of herbs was compared (*t* test) with woody plants by comparing the differences from the data for paired plots for herbs with the differences from the data for paired plots for the woody plants. By breaking the woody plant data into trees and other (mostly shrubs) and comparing the differences of herbs, trees, and other woody plants by a one-way analysis of variance, the relative importance of these three groups in invading the habitat could be assessed.

Several experiments that crossed habitat lines were performed. Four pairs of plots on the upland (upland *Hedera* and natural understory

*Lonicera*) containing *Podophyllum peltatum* (mayapple) were analyzed by a *t* test. The other experiments compared different habitats: *Parthenocissus quinquefolia* was compared in the two *Lonicera* habitats by a *t* test, and herbs, woody plants, trees, and other woody plants (mostly shrubs) were each compared in all four habitats by a one-way analysis of variance.

Some of the statistical tests required modification, and in all cases count data were square root transformed ( $\sqrt{x + 0.5}$ ) before analysis.

The treated plots, as mentioned earlier in discussing the determination of ecological dominance by biomass, were cut around their perimeter to a depth of about 15.2 cm. To ensure a valid comparison with the control plots that could not be attributed to increased water from lack of root competition, the perimeters of the control plots were cut to the same depth at the same time. In other words, all plots were trenched. The control and treated plots were read at the same time during the season of trenching and biomass removal and read again about a year or more later. The count data were transformed and the difference between the first and second reading on the control plots was compared by a paired plot *t* test with the difference between the first and second readings on the appropriate treated plots. The actual dates of plot readings were as follows: upland *Hedera* herbs read 1 and 25 June 1971 and again 22 and 23 May 1972; upland *Hedera* woody plants read 31 March 1971 and 14 August 1972; natural understory *Lonicera* herbs read 1 and 25 June 1971 and again 16 May 1972; natural understory *Lonicera* woody plants read 31 March and 1 April 1971 and 16 August 1972; flood-plain *Hedera* herbs read 1 and 25 June 1971 and 18 May 1972; flood-plain *Hedera* woody plants read 1–5 April 1971 and 15 August 1972; and cleared understory *Lonicera* herbs and woody plants read 12 and 13 April 1971 and 12–15 May 1972 (herbs) and 15 August 1972 (woody). The reading of certain plots on 1 June and again 25 June 1971 was to assure coverage of early and late spring herbs. The procedure was found unnecessary and not continued in 1972.

*Replacement of Exotic Iris.* To learn more about the decline of *Iris* and the species replacing it, several surveys and experiments were done.

1. Surveys. All surveys were conducted on control plots using frequency data from the 100 dm<sup>2</sup> grid as previously described. When the vegetation was high, the meter square frame with the grid was placed on stilts over the plot to be read. All species that occurred in the plots were tallied by frequency (presence or absence in each square decimeter as previously explained).

Two surveys were made of the *Iris* decline: one in the open marsh plots and one in the swamp-marsh transition plots. In each case, the plots were examined over a period of time to obtain a pattern that could be shown on a line graph. In each case, frequency data were available

from the April 1971 and April 1972 control checks. Data were also available from three open marsh plots 10–14 June 1972 and from four swamp-marsh transition plots 3–6 May 1972. These were the times when the annual biomass growth would have been collected from the treated plots. On 1 and 2 August 1972, frequency was tallied from the herbaceous overstory of the 13 control plots in the swamp-marsh transition *Iris* and on 11 and 12 August 1972, the 7 control plots in the open marsh *Iris* were surveyed in the same manner. Because the records as well as general observation showed *Peltandra virginica* to be obviously more abundant than other species, the *P. virginica* data were treated in the same manner as *Iris pseudacorus*.

Two line graphs were drawn: one for the open marsh *Iris* habitat and one for the transition *Iris* habitat. On each graph, the average frequency was plotted against time for both *Iris* and *Peltandra*, after each point was shown to be significantly different from the preceding point. Chi-square analysis of  $1 \times 2$  tables was used to determine significance between points. Because the *P. virginica* data had to be analyzed separately from the *I. pseudacorus* data, they were considered as separate surveys. The following comparisons were made for the two species in the transition area: April 1971 and April 1972 by pooled chi-square for *Iris* and individual chi-squares for *Peltandra* on all 13 plots (and verified by pooled chi-square using only the four plots associated with annual biomass collection); April 1972 and May 1972, and May 1972 and August 1972 by the individual chi-squares on the same 4 plots; and April 1972 and August 1972 by individual chi-squares on all 13 control plots. The comparisons for the two species in the open marsh *Iris* habitat were similar: April 1971 and 1972 by individual chi-squares of the seven control plots for *Iris* and pooled chi-square for *Peltandra* (and verified by individual chi-squares for *Iris* and pooled chi-square for *Peltandra* using only the three plots associated with annual biomass collection); April and June 1972 by individual chi-squares on the same three plots; June and August 1972 by pooled chi-square for *Iris* and individual chi-squares for *Peltandra* on the three plots; and April and August 1972 by individual chi-squares on all seven control plots.

Because the *Iris* in the transition began declining later than in the open marsh and the *Iris* in the open marsh had already declined to almost zero, the following series of comparisons by *t* tests on arc-sine transformed data between the two habitats were made to determine whether the transition *Iris* had the same pattern and would soon decline also: transition of April 1972 with marsh of April 1971, transition of May 1972 with marsh of April 1972, transition of August 1972 with marsh of June 1972, and transition of August 1972 with marsh of August 1972. Some of the *t* tests were modified.

Comparisons were made for *Peltandra* between the two habitats on a contemporary basis, i.e., transition of August 1972 with marsh of



August 1972, transition of May 1972 with marsh of June 1972, and transition of April 1972 with marsh of April 1972. No statistical comparison was needed for the transition of April 1971 (which had a frequency of one in only one plot) with marsh of April 1971 (which had no *Peltandra*).

2. Germination Tests. As another means of evaluating *Iris pseudacorus* and *Peltandra virginica* relationships, germination tests were made on 225 seeds for each species. *Iris* seed was collected 13 October 1971, and *Peltandra* seed was collected 4 April 1972.

After consulting several texts and finding no specific information on seed dormancy for these species, they were treated as follows. The *Iris* seed was stored dry in an unheated laboratory room which was 5–11° C above winter outdoor temperatures. On 22 March 1972, they were soaked in cold tap-water for 24 hours and received moist stratification at 4–5° C beginning 23 March. On the morning of 12 April 1972, they were soaked in river water at room temperature and 60 hours later (14 April), they were placed in the refrigerator (in the same water) at 4–5° C. The *Peltandra* seeds were refrigerated in moist marsh muck 5 April 1972 at 4–5° C.

The seeds were planted 18 April 1972 in 25, 17.5-cm-high cans, each of which was two-thirds full of wood chips with autoclave-sterilized marsh soil on top to within 2.5 cm of the lower edge (cans were on a gently sloping roof). Eighteen seeds were randomly placed in each can by use of a random digits table. Five cans each of the following proportions were planted: all *Iris*; all *Peltandra*; two-thirds *Iris*, one-third *Peltandra*; one-third *Iris*, two-thirds *Peltandra*; half *Iris* and half *Peltandra*. This investigation originally was to have been a competition experiment, but as it became evident that germination conditions for each species were entirely different, the experiment was changed to germination testing.

The seeds were inundated in the cans almost continuously for 97 days with either river water from the Potomac or rain. The nutrient composition of the water would be expected to vary from one watering to the next as under natural conditions, but each watering would be uniform within itself. At 97 days, a germination count was made. The water was allowed to evaporate naturally until the soil was only moist and then maintained at the moist level for 90 days. At the end of 90 days another germination count was made.

The germination percentage and confidence limits at the 0.05 level were determined for each species, and the significance of the difference between the two germination proportions was computed.

3. Competition Experiments. The transition *Iris* area is associated with *Acorus calamus*. Two competition experiments between *I. pseudacorus* and *A. calamus* were set up in a 5 × 5 Latin square experimental design and analyzed by analysis of covariance on logarithmic [ $\log(x + 1)$ ] transformed data. Although many competition experiments use seeds,

these used rhizomes. The covariance analysis accounts for the fact that rhizomes will be of varying weights at the start of the experiments.

Rhizomes with attached leaves were collected 10 April 1972 for the two species. On 11 April they were washed and 75 rhizomes, about 2 cm in diameter, of each species were selected. These 150 rhizomes were cut, when necessary, to a 10 cm length. They were planted, six rhizomes to a basket pot, in autoclave-sterilized marsh soil. There were five basket pots, each of the following proportions: All *Iris*; two-thirds *Iris*, one-third *Acorus*; half *Iris*, half *Acorus*; one-third *Iris*, two-thirds *Acorus*; and all *Acorus*. The live or fresh weight of each species in each basket pot was determined prior to planting to the nearest 0.01 g on a triple beam balance. The data were rounded to 0.1 g. The plants were watered with Potomac River water when sufficient rain did not do the job. The plants were not continuously inundated. The experiments were discontinued 28 September 1972, at which time the fresh weight of each species in each basket pot was again weighed as described above. Although both species were in the same setup, they had to be analyzed separately, hence they are two experiments. The one experiment was conducted to determine the impact of *Iris* on *Acorus*, and the other to determine the impact of *Acorus* on *Iris*. Significance was set at the 0.05 level.

### Limiting Factors

Surveys and experiments were conducted to determine some factors which may be limiting or promoting the spread of the three exotic species under study. The factors selected for study were light, vegetational strata, water, vegetation, and soil.

*Light as a Limiting Factor.* Light was investigated both by surveys in different habitats and by experiments.

1. Light in Different Habitats. Ozalid meters (Friend 1961) with GAF Ozalid 402 IZE sepia intermediate paper were used to measure the light in habitats with the exotic under study and in similar habitats without the exotic. The meters were sealed with 2.5-cm wide polyethylene weatherstrip tape. The booklet of sepia paper could not be read or estimated accurately to give ten "between paper" divisions as mentioned by Friend (1961). With the paper used in this experiment, estimates 0.25, 0.50, and 0.75 of a paper could be made consistently.

Light was measured at each of the 126 light stations at least 8 days in the year: autumnal equinox, winter solstice, vernal equinox, summer solstice, and halfway between each of these points. The exact dates were taken from the U.S. Coast and Geodetic Survey (1970:269) and National Ocean Survey (1971:269) publications. Because many of the meters were under water at the summer solstice (flood from Hurricane Agnes), the light measurements were retaken a few days later. In the



forested areas, light was measured 23 September, 7 November and 22 December 1971, 4 February, 20 March, 5 May, 30 June, and 7 August 1972. The light measurements on the marsh and swamp-marsh transition areas were started later beginning with 7 November; the eighth measurement was 22 September 1972.

The meters were placed in position the day before the light measurements were to be taken, except at the well-visited memorial area, and covered with cans (often held in place by a stick). One hour before sunrise (U.S. Coast and Geodetic Survey 1970:253; National Ocean Survey 1971:253) on the day of measurement, the meters were uncovered and those on the monument bridges were set out. This operation lasted no longer than 1 hour after sunrise. After being out for 24 hours (suggested by Friend 1961: 578), the meters were covered the next day at the same time and in the same order and the meters at the memorial removed. The next several hours were spent retrieving the rest of the meters for processing at the laboratory.

The open field was selected as the standard for open sunlight, but as a check to assure that the lights from the nearby highway bridge would be innocuous to the surveys, light readings were also taken at the monument. Light readings were taken at both the open field and the monument bridge (memorial area) whenever light measurements were taken for the other habitats. For each date, the light measurements for the field were compared by a  $t$  test with the light measurements taken at the memorial. Because the number of papers bleached is proportional to the logarithm of light energy received (Friend 1961:579), the data were transformed to antilogarithms before analysis. Some  $t$  tests were modified. There was no significant difference at the preset 0.01 level between the field and the memorial for any date.

With the average paper reading of the 10 open-field stations as a base, the other 96 station readings were converted to a percentage of open sunlight. Each of the eight seasonal readings was compared separately; therefore, the base number for determining percentage was different for each season. The forested areas were compared together and the marsh areas were compared together at each season by a one-way analysis of variance on arc sine transformed data.

2. Light and Biomass in the Upland Forest. Another way of evaluating the importance of light is to see what correlation exists between the percentage of open sunlight and the amount of biomass produced at a site. This was done for *Hedera helix* and *Lonicera japonica* both on a total biomass basis and an annual biomass basis. Total biomass came from the original biomass removal from the 1.25-year plots. Biomass was rounded to the nearest whole gram. Percentage light was from the average from each station for the year. The base number for determining per cent was the average number of paper readings for the 80 measurements taken over a period of 1 year for the 10 light stations in the open

field. Percentages were rounded to the nearest whole number. The year of light values was not completely coincidental with the year of annual growth. Both *Lonicera* areas were used in the *Lonicera* regressions, but only the upland *Hedera* area was used in the *Hedera* regressions.

3. Controlled Shade and Light Experiments. Fourteen experiments were conducted on each of the two physical designs (*Hedera* and *Lonicera*) with shade controlled by layers of cheesecloth (total of 28 experiments): (dependent variable stated first) chlorophyll A and shade, chlorophyll B and shade, total chlorophyll and shade, leaf biomass and shade, vigor and shade, leaf biomass and vigor, total chlorophyll and vigor, total chlorophyll and leaf biomass, shade and light, chlorophyll A and light, chlorophyll B and light, total chlorophyll and light, leaf biomass and light, and vigor and light.

The experiments for each species consisted of a control and four other treatments, each control and treatment being replicated three times: a total of 15 plots  $1 \times 1$  dm. The experiments were begun 27 August 1972; vigor experiments were terminated 31 October, all the other *Lonicera* experiments were terminated 25 November, and all the other *Hedera* experiments were terminated 2 December 1972.

Vigor was estimated in square centimeters of green or yellow leaves in each square decimeter plot. The data analyzed are an average of an estimate made on 26 October and one made 31 October. All plots were  $100 \text{ cm}^2$  of healthy *L. japonica* or *H. helix* at the beginning of the experiments.

Shade was counted by the number of layers of cheesecloth wrapped around the wire baskets.

Leaf biomass was measured in number of grams dry-weight per square decimeter after the chlorophyll had been extracted. After chlorophyll extraction, the biomass was oven dried at  $70 \pm 1^\circ \text{C}$  for 42 hours for *Lonicera japonica* and at  $68 \pm 1^\circ \text{C}$  for 43 hours for *Hedera helix*. The biomass was weighed on an electronic balance (Mettler H54) to five digits to the right of the decimal point.

Chlorophyll was extracted for each square decimeter plot by grinding the leaves with a pestle and mortar in 80% (by volume) acetone (20% distilled water). The leaf biomass and aqueous acetone were set in a dark refrigerator ( $2\text{--}3^\circ \text{C}$ ) over 2 nights for *Lonicera* and 3 nights for *Hedera*, centrifuged for 15 minutes, and decanted. More aqueous acetone was added to the biomass and placed in the refrigerator over 1 night; this was followed by a 15-minute centrifuging and decanting. With *Hedera*, the process was repeated a third time to obtain complete extraction of the chlorophyll.

The leaf biomass was dried and weighed as described above.

The chlorophyll extract volume was measured in milliliters, diluted in a 1:5 ratio (1-ml extract, 4 ml 80% acetone) and the per cent transmittance read at  $663 \text{ m}\mu$  for chlorophyll A and  $645 \text{ m}\mu$  for chlorophyll

B on a multipurpose recording spectrophotometer (Shimadzu MPS-50L). A program was available (using formulas from Arnon 1949) for a programmable calculator (Monroe Model 1785) which converted the transmittance, diluted extract volume, and leaf dry-weight data to micrograms of chlorophyll A, B, and total chlorophyll each per gram of dry weight of leaf biomass. For experimental analyses, micrograms were converted to milligrams to the nearest tenth.

Light was measured in each square decimeter plot on three randomly selected (random digits table) days (22 September, 3 and 9 October 1972) in the same manner as previously described for light measurements. On each of these days, the 10 light stations in the open field were operated, thus the experimental readings were converted to per cent (to two digits to the right of the decimal point) of open sunlight. An average light measurement for each square decimeter plot was obtained by averaging the percentages of these 3 days.

To determine the influence of different degrees of shading by cheese-cloth on chlorophyll A, chlorophyll B, total chlorophyll, leaf biomass, and vegetation vigor, an analysis of variance was computed for each of these randomized block design experiments with both *Lonicera* and *Hedera*. For further clarification, a regression was also computed for each experiment. The *Hedera* vigor and shade experiment presented problems; the "no-shade" data had to be eliminated to make the data homogeneous for both the analysis of variance on the randomized block design experiment and the regression.

To determine the influence of vigor on leaf biomass and on total chlorophyll, leaf biomass on total chlorophyll, light on shade, and light on each of chlorophyll A, chlorophyll B, total chlorophyll, leaf biomass, and vigor, the data were analyzed by linear or curvilinear regressions for model I regression design experiments.

*Vegetational Strata (Structure) as a Limiting Factor.* Because there is a relationship between light and the vertical structure or stratification of vegetation (Billings 1970:72; Oosting 1956:21), community structure was examined in both exotic and nonexotic areas with woody strata for number and proportion of strata, and association of one stratum with another (both qualitative and quantitative).

Basic to these investigations was a simple random sampling survey in each vegetational type (from 20 April to 12 June 1972) to determine the actual layers present. At each of the random points (see *The Placement of Vegetational Strata Stations* under *The Physical Setup* above), the height of every plant that occurred directly over each point was measured either with a meter stick or a Merritt hypsometer. The original measurements in logs, feet, meters, or centimeters were converted to meters. A line graph was then prepared for each of the nine habitats surveyed. The height of each plant was plotted by sampling point and



labeled by species. The uppermost permanent height in each stratum in each habitat was delineated by a line that connected the appropriate points. Plants that had the potential of growing out of a given stratum played no part in defining the strata but were used in the various analyses. In many instances, the lines or parts thereof were immediately placed because of the obvious pattern of points. Every stratum is not represented at every point, and some strata are not uniformly at the same height. Because of these conditions, the potential height of some species needed to be determined; this was particularly true in differentiating some sections of overstory and understory trees. To obviate this problem, potential height of the species in question was first looked for in the habitat under study. Failure here resulted in looking at the other habitats on the island. Lastly, several texts were consulted as needed: Fowells 1965; Gleason 1952; Fernald 1950; Harlow and Harrar 1950; Hough 1936.

The validity of both a ground layer (low herb layer) and a tall herb layer in the upland forest without the exotics was tested by a  $t$  test.

1. Number of Strata. The ground layer with and without exotics was tested on the flood plain by a modified  $t$  test and on the upland forest areas (four habitats) by a modified one-way analysis of variance.

For each habitat, the number of strata present (whether temporary or permanent) at a given point was compared by chi-square in a  $1 \times 2$  table against the expected number in the same habitat as determined by the previously constructed graphs. The habitats were also compared in a similar manner but with the expected number being determined by the layer number in a similar habitat that contained no exotics. Pooled chi-square was used for each of the nine habitats except where the heterogeneity chi-square was significant, in which cases the individual chi-square for each sampling point had to be analyzed.

The swamp was included in this structural study because of its proximity to the swamp-marsh transition, and yet it contains no *Iris pseudacorus*.

2. Qualitative Association of Strata. Is the exotic ground layer correlated with the presence or absence of another stratum of vegetation? In each habitat rather than compare every layer with only the ground layer where the exotic in question occurs, a more complete view was hoped for by comparing every layer against every other layer in all possible combinations to answer the question, does one layer affect the occurrence of another layer or alternatively are they independent of each other? This was done in  $2 \times 2$  contingency tables. Exact probabilities were determined for a two-tailed test. In addition, the tetrachoric coefficient of correlation was estimated for each table.

After each of the nine habitats had been analyzed separately, the data were combined in the following ways and analyzed by comparing every layer against every other layer in all combinations: all five-layer forests, terrestrial forests (no swamp), flood-plain forests, upland forests, no-

exotic forests, exotic upland forests, swamp-marsh transition area (all four-layer forests). The analysis used pooled chi-square except where heterogeneity was significant. The tetrachoric coefficient of correlation was estimated for each of these seven surveys.

3. Depth of Woody Strata (Quantitative Association of Strata). Another approach to the subject of the relation of one layer to another was to measure the depth of the woody (tree and shrub) layers over each sampling point (20 April–12 June 1972). The lower layers had no appreciable depth that could be measured over the points. With the shrub layer as the dependent variable and the overstory and understory as independent variables, each of eight habitats (not enough data for cleared understory *Lonicera*) was analyzed separately by a multiple straight line regression. Each regression was tested by an analysis of variance (F test). The coefficient of multiple determination was also calculated for each.

In addition, simple linear regressions, tested by *t* test, were computed for all three combinations of variables in each of the eight habitats. The coefficient of determination was computed for each of these.

After each of these eight microvegetation types had been analyzed separately, they were analyzed in pairs by discriminant function (essentially a way to compare two multiple regressions) and tested by analysis of variance. The following seven comparisons were made to determine whether there were significant differences in structure of the upper three layers between habitats: no exotic forest with each of upland *Hedera*, natural understory *Lonicera*, cleared understory *Lonicera*; no exotic flood plain with flood-plain *Hedera*; no exotic swamp-marsh transition with transition *Iris*; and swamp with no exotic transition; and swamp with transition *Iris*.

*Elm Depopulation as a Factor in Exotic Vine Spread.* Three surveys were conducted (from 10–14 October 1972), ultimately to answer the question of whether elm (*Ulmus americana*) removal is associated with the increase in the exotic vines of *H. helix* and *L. japonica*. These surveys were censuses made in which the data were recorded on McBee Keysort cards.

The first of these censuses was a survey of all standing and alive overstory *Ulmus americana*. Each of the 187 trees was recorded as having no exotic vines, *H. helix* only, *L. japonica* only, or both vines. The data were converted to the nearest whole per cent for each of these categories. There are no probability statistics needed when a complete census is done; however, by treating the census as a sample, confidence limits for elms with and without exotic vines were determined from a table for binomial distribution at the 0.05 and 0.01 level.

The data from the other two census surveys were cross-classified across the classes of the dependent variable, placed in analytical (text)



tables, and converted to the nearest whole per cent. The tables were then analyzed as described by Neter and Wasserman (1961:97–115). For one of these two surveys, a census was made of all nonvigorous, standing, overstory trees. The 429 trees were designated as *Ulmus americana* (the only *Ulmus* on the island) or other (all other species), the vigor as either dead or dying (one or more dead main branches), and the infestation (dependent variable) as no exotic vines, *Hedera helix* only, *Lonicera japonica* only, or both vines present on the same tree.

The other survey was a census of all canopy-size fallen trees on the island. Again, the trees were classified as *Ulmus* or all others. Each of the 516 trees was classified as to whether it was cut down or fell naturally, and the dependent variable, kind of infestation, was classified into 15 categories. These 15 categories classified the exotic species (one, both, or neither) that were growing on the logs and when the exotic became associated with the trees, i.e., before it came down, after it came down, or both.

The time in which the exotic vine became associated with the log, whether before or after the tree came down, was determined by the direction of vine growth, whether essentially longitudinally with the trunk (if it occurred before the fall) or transversely on the trunk (if it occurred after the fall). After the raw data were collected, it was found that some categories had no data; therefore, these categories do not appear in the results.

*Duration of Water Inundation as a Limiting Factor for Iris.* The duration of water inundation was studied by examining the topographic elevations in the marsh and the river discharge levels.

1. Topographic Gradient. The relative duration of water inundation of *Iris* was investigated in an indirect manner by determining the topographic slope of the marsh area. The higher areas would be expected to receive a shorter period of water inundation by the tide. All elevations in the marsh area were measured 21–23 September 1972.

The elevation of the 10 non-*Iris* swamp-marsh transition-zone light stations and the 10 stations on the bank nearest these light stations was measured by rod and level to the nearest 0.001 ft and converted to meters. The elevation of each of the 10 bank stations was plotted on a graph against its nearest neighbor tree-line (transition) station to determine whether the points all fall on one side of a 45°-angle line drawn through the origin, thus indicating a slope. This slope was verified by a *t* test which compared the gut stations with the transition stations. To determine whether the marsh sloped from head to mouth, the five transition stations and their associated gut stations on the headward end were compared by a modified *t* test with the stations toward the mouth end.

To ascertain whether *Iris* grows at higher elevations than other marsh

vegetation, the elevation of each non-*Iris* light station and each *Iris* control plot was measured to 0.001 ft and converted to meters. The four groups—open marsh *Iris*, open marsh non-*Iris*, transition *Iris*, transition non-*Iris*—were compared by a modified analysis of variance for a completely randomized survey.

2. *Iris* Biomass, Light, and Elevation. The influence of both light and elevation on *Iris* biomass was ascertained by comparing the data in a multiple straight line regression, and then in two simple straight line regressions. The multiple regression was tested by an analysis of variance and the simple regressions were tested by a *t* test. The following coefficients were computed: multiple determination, partial determination, determination. The significance of the coefficients of partial determination was tested by *t* tests.

The light values used in the analyses were the average light measurements for each station for the year, then converted to per cent (to three digits to the right of the decimal point). It would have been a little better to have measured the elevation on the same plots from which the biomass was taken, but it was the unexpected turn of events that led to this survey; therefore, the elevations were taken from the control plots associated with the biomass plots as previously described. (The biomass plots without the biomass were noticeably lower in elevation.) The dry weight biomass was determined as described earlier.

3. River Discharge. Water discharge data of the Potomac River in cubic feet per second (cfs) near Washington, D.C., were obtained from the U.S. Geological Survey (1972). The gauge is located about 8 km upstream from Theodore Roosevelt Island. The total discharge (cfs) for the growing season, April through September, was determined from 1962 through 1971. The total discharge for March through June 1971 was compared with the same months in 1972 with a *t* test. The data were collected by someone else and appear to have been rounded; therefore the significance level was lowered to 0.05 for this physical measurement.

*Vegetation as a Limiting Factor for Iris.* To learn whether *I. pseudacorus* was actually growing in a different vegetation type than the non-*Iris* areas, the dominant plant at each of the 40 light stations in the marsh areas 21–23 September 1972 was sampled. This was after the *Iris* had begun to die out. *Peltandra virginica* occurred more often (35%) and had larger plants, so it was used in analyzing the following surveys: presence or absence of *Peltandra* at *Iris* and non-*Iris* stations; presence or absence of *Peltandra* in open marsh with and without *Iris*; presence or absence of *Peltandra* in the transition with and without *Iris*; and presence or absence of *Peltandra* in open marsh or in the transition. The data were placed in  $2 \times 2$  contingency tables and analyzed by chi-square. The tetrachoric coefficient of correlation was estimated from a table for each of the four surveys.

*Soil as a Limiting Factor for Iris.* Two aspects of soil were examined 21–23 September 1972 in the marsh areas from the control plots: soil color as an indication of oxidation, and whether a hardpan is present or not. A 20-cm core of soil was taken from the center of the *Iris* control plots and from the light stations in the non-*Iris* areas. The soil auger bit is about 3 cm in diameter. When boring became difficult due to compacted soil (which was clay), the soil was classed as hardpan. Soil that was gray, black, greenish, or bluish-gray was considered reduced (gley), and that which was red, yellow, brown, brownish-black, or mottled was considered oxidized (not gley).

In one set of four analyses, the soil was classified as mostly gley or mostly not gley in the following habitats and habitat combinations: *Iris* and no *Iris* areas; open marsh with and without *Iris*; swamp-marsh transition with and without *Iris*; and transition and open marsh areas. In the other set of four analyses the soil was classified as hardpan present or absent in each of the above-listed habitats or combinations. In all eight of these surveys, the data were placed in  $2 \times 2$  contingency tables and analyzed by chi-square with and without Yates' correction for continuity. One case required computation of exact probabilities. From a table, the tetrachoric coefficient of correlation was estimated.

### *Miscellaneous Observations*

During the course of investigation, unexpected observations which were related to the objectives of the study were recorded.

### 3

## Results

### *Importance of the Exotics in Different Habitats*

#### Ecological Dominance

One result of the investigation of dominance by determining biomass (Table 2) shows that, among the exotics, only *Hedera helix* is as important in one habitat as in the other. Another result is that among the three species in their two habitats each, there are four levels or degrees of impact in the following order: transition *Iris* (greatest), *Hedera* and open marsh *Iris*, cleared understory *Lonicera*, and natural understory *Lonicera* (least). Frequency was tried as a quick way of assessing dominance. As shown by comparing Table 3 with Table 2, this method does not come close when dominance is being compared among different species or within the same species in different habitats. The intermediate



*Hedera helix* on the ground and climbing trees on the upland near the controlled shade and light experiments with this species.



method (in time consumption) of comparing dominance by examining cover (on *H. helix* only) appears to have some merit under some conditions (Table 4). Had the significance level for the modified *t* test been set at the same minimum level as for the modified analysis of variance, the conclusion would have been that there is no significant difference between *H. helix* in the two habitats, thus agreeing with the biomass determinations. The controlled shade experiments (Tables 74 and 75) showed a high correlation of leaf biomass with cover (vigor) for both *H. helix* and *L. japonica*.

### Growth Rate

Another way of assessing the impact of these exotic species is to determine how fast they can synthesize biomass from their environment. Table 5 indicates that *L. japonica* in the cleared understory habitat is a relatively faster grower than the others (note level of significance for a shorter period of time). The 1.25 years' biomass of the flood-plain *Hedera* was collected after the flood of Hurricane Agnes. The experimental results in Table 6 (one year of biomass) support the results in Table 5 in showing the cleared understory *Lonicera* with the greatest biomass. Further ordering of biomass classes shows *H. helix* in the upland to have the second largest biomass accumulation in a year, and flood-plain *Hedera* and natural understory *Lonicera* are tied for third place. The experiment of Table 7 (comparison of 1.25 years of growth) verifies that upland *Hedera* is a faster grower than *Lonicera* under a natural understory. The fact that the flood-plain *Hedera* 1.25 years' biomass was collected after the hurricane flood along with its low mean was the clue to computing a *t* test for further clarification.

Growth rate determinations from tallying frequency of occurrence on a 100 dm<sup>2</sup> grid were not wholly satisfactory as can be seen by comparing Tables 5 through 7 with Tables 8–18. Some results support the biomass results and some do not; still other results, particularly comparing habitats (Tables 17 and 18) on either a 1 year or 1.25 years' basis, tend to obscure the relative importance of the species in different habitats compared with the biomass basis (Tables 6 and 7).

The determination of cover as a means of evaluating growth rate was better than the use of frequency (compare Tables 5–7 with Tables 19–22). The only discrepancy is with the upland *Hedera helix*. There is a significant difference in cover between 1 year of growth and 1.25 years of growth (Table 19), whereas there is no significant difference on a biomass basis (Table 5).

### Importance of English Ivy on the Flood Plain

The flood from Hurricane Agnes rose about 4 m above mean sea level (Table 23). This altered some of the experiments. *Hedera helix* biomass



on the flood plain was less at 1.25 years of growth than at 1 year of growth (Table 5); this requires a modification of the kind of conclusion that normally might be drawn from the data in Table 7. However, flood plains are subject to floods and by means of surveys and an experiment, the relative importance of *H. helix* was assessed. It was found that differing amounts of ground cover (mostly *Hedera*) had no influence on the deposition of mud (Table 24). This being the case, additional random observations from the pair of plots and at the light stations in the flood plain were combined with those from the randomized block design experiment to give a mean depth of almost 8 cm of mud deposited on the island (Table 23).

The frequency data and conclusions were verified by that of cover in showing *H. helix* "decline" from the flood (Tables 25 and 26). The decline was significant beyond the 0.001 level. This is a relatively greater decline as assessed by significance level than other (mostly native) plants (0.1–0.025) of the flood plain (Table 27). Note that there is no significant difference between survival of woody and herbaceous plants. The woody plants did not include mature trees.

## *Replacement of One Species or Life Form by Another*

### **Replacement of Native Life Forms and Species**

The results of the plot-weeding experiments in the upland *Hedera helix* (Table 28) indicated that the exotic had a greater influence (suppression) on herbs than on woody plants (note the means, *t* value, and significance levels). This idea was verified by comparing herbs with woody plants (significance beyond 0.001). Among the woody plants as a group, the data indicated (Table 28) that shrubs (including woody vines) and trees are probably about equally influenced by the exotic (note "other woody" significant at 0.1 and trees not significant at this level). This hypothesis was verified as well as the ascendancy of herbs compared with woody plants when the three life forms were compared (Table 29).

The plot weeding experiments in the natural understory *Lonicera japonica* show that this vine influences woody plant growth more than it does the herbs (Table 30). The verifying experiment (herbs vs. woody plants) failed to substantiate this conclusion in general, but note the discrepancy in plot replications for each group. Replications for woody plants are almost three times that of the herbs. Although the experiment for trees would at first indicate they have suffered more than shrubs and woody vines (other woody), the *t* values indicate there may not be a big difference. The verifying experiment (Table 31) shows no significant differences in the influence of *L. japonica* under a natural understory on life forms.

Experiments on two species in the natural understory *Lonicera*, *Prunus serotina*, and *Parthenocissus quinquefolia*, had results in these particular cases similar to that of trees and other woody plants, respectively (Table 30).

*Podophyllum peltatum* occurs on the upland of the island and was found in both *Hedera helix* and *L. japonica* plots. A paired-plot design experiment of only four replications failed to demonstrate any significant influence of exotic vine growth on this particular native species (Table 32).

The plot weeding experiments in the flood-plain *H. helix* show that English ivy has no significant influence on the woody plants collectively, but that it does have a significant influence on the herbs (Table 33). (The verifying experiment (herbs vs. woody plants) does not show a significant difference in impact on these life forms.) When the woody plants are separated into trees and other woody plants, the experiments fail to demonstrate that removing the exotic made any significant difference. The experiment shown in Table 34 verifies these conclusions (5% Duncan's test) by showing herbs significantly different from the woody plants, although the woody plants are not significant among themselves. However, it may be noted that the woody plant experiments were completed after the flood of Hurricane Agnes. There was apparently no significant difference between woody plants and herbaceous plants as influenced by the flood (Table 27). The flood had a greater impact on woody plants than *Hedera helix* had on woody plants (see means, *t* values, and significance levels).

Some clarification was sought by dividing the flood-plain herbs into two groups and an experiment performed on each. Neither group benefited by the *Hedera* removal (Table 33).

One result of removing *Lonicera japonica* from the cleared understory area was that the herbs benefited more than woody plants as a group (Table 35). The verifying experiment (herbs vs. woody plants) substantiated that conclusion. Clarification was sought by separating the trees from the other woody plants for experiments. The trees benefited greatly by the removal of this vine while the other woody plants (shrubs and woody vines) were not significantly influenced. This would indicate that herbs, trees, and other woody plants in that order would be influenced by *L. japonica* in the cleared understory area. The verifying experiment substantiates this biologically (Table 36). Note that the large, significant variance necessitates biological rather than statistical differences.

Besides the life forms, a number of individual species were investigated in the cleared understory (Table 35). None of the woody vines (*Parthenocissus quinquefolia*, *Rhus radicans*, *Vitis rupestris*) was influenced by the removal of *L. japonica*. All the trees (*Liriodendron tulipifera*, *Ulmus americana*) and one herb (*Oxalis stricta*) were significantly ben-

efited by the action. The other herb (*Allium vineale*), a native of Europe (Gleason 1952, 1:413), was not benefited by the action.

*Parthenocissus quinquefolia* occurs not only in the cleared understory *Lonicera* (Table 35) but also in the natural understory *Lonicera* (Table 30). The large discrepancy in *t* values indicated that *L. japonica* may have a greater influence on this native vine under a natural understory. The verifying experiment substantiates that position (Table 37).

Several comparisons were made between different habitats to determine whether the exotic vine removal was correlated with a greater influx of given life forms in one area than another. From Tables 28, 30, 33, and 35, it would appear that *Hedera* and *Lonicera* have different influences on herbs depending upon the habitat, with the greatest being in the upland *Hedera* and the least in the natural understory *Lonicera*. A completely randomized design experiment verified this conclusion and showed the differences to be significant (Table 38). Tables 28, 30, 33, and 35 indicate that the exotic vines under study have almost an equal influence on woody growth collectively, with the possible exception of the natural understory *Lonicera* being different from the flood-plain *Hedera* and the cleared understory *Lonicera*. The experiment to test this is shown in Table 39 and shows no differences between habitats.

The influence of *H. helix* and *L. japonica* on the tree life form is indicated by Tables 28, 30, 33, and 35 to be in the following habitat order: cleared understory *Lonicera* (greatest influence here), natural understory *Lonicera*, and then both *Hedera* habitats. The experiment to test this verifies no differences between the *Hedera* habitats (Table 40), but other aspects of the hypothesis were modified as shown.

In a similar manner, a prediction was made for the other woody plants (mostly shrubs and woody vines) that there would be no significant differences between the upland *Hedera* and the natural understory *Lonicera* nor between the other two habitats, but the two sets of habitats would differ from each other (Tables 28, 30, 33, and 35). The experiment to test this verifies part of the prediction (Table 41).

### Replacement of Exotic *Iris*

The *Iris* "die-off" disrupted experiments which were planned to parallel those of *H. helix* and *L. japonica* just considered. Surveys were substituted. Figure 2 shows that *I. pseudacorus* increased in the swamp-marsh transition zone before it decreased. It also shows that during the *Iris* decline, *Peltandra virginica* (the most abundant plant of the plots) began to increase in importance. Tables 42 and 43 summarize the statistical analysis of the points plotted in Fig. 2. In other words, the points plotted in the figure are considered real and not artifacts of the data.

Figure 3 shows the results of the open marsh surveys in a similar

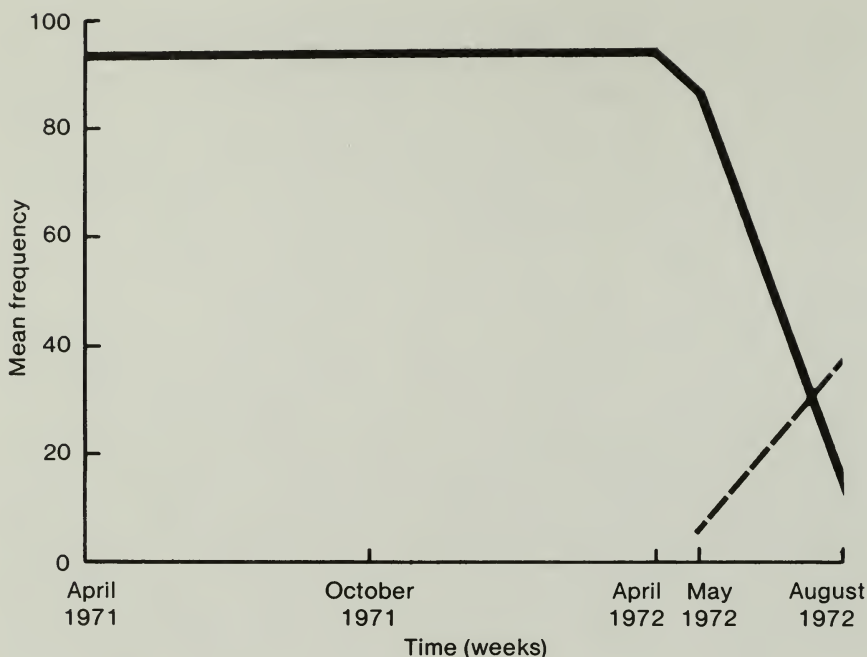


Fig. 2. Comparison of swamp-marsh transition *Iris pseudacorus* (solid line) and *Peltandra virginica* (broken line) by mean frequency per square meter against time.

manner, and Tables 44 and 45 summarize the statistical support for the line graph.

Note that in the marsh *Iris pseudacorus* has decreased to zero (average). It would appear from the graphs that the transition *Iris* is following the same pattern as that in the marsh, except that it has started later. This was tested by matching the dates and testing the mean frequencies per square meter as shown in Fig. 4. The decline patterns do match. The statistical summary for this figure is shown in Table 46.

A similar comparison was made for *Peltandra virginica* but the points compared were contemporary in time as the graphs in Figs. 2 and 3 indicate they should be. The diagram of Fig. 5 indicates that *Peltandra* increases uniformly without regard for open or transition areas. The statistical summary to support this diagram is in Table 47.

To elucidate *Iris* and *Peltandra* relationships, a competition experiment was set up; but as mentioned in Materials and Methods, it was a failure because as long as the seeds were well watered only *Peltandra* came up and when the soil was kept only moist, *Peltandra* died out and *Iris* came up. That was an important failure because it indicated that inundation by water was a limiting factor in *I. pseudacorus* growth. This is described later along with other limiting factors of the three exotic



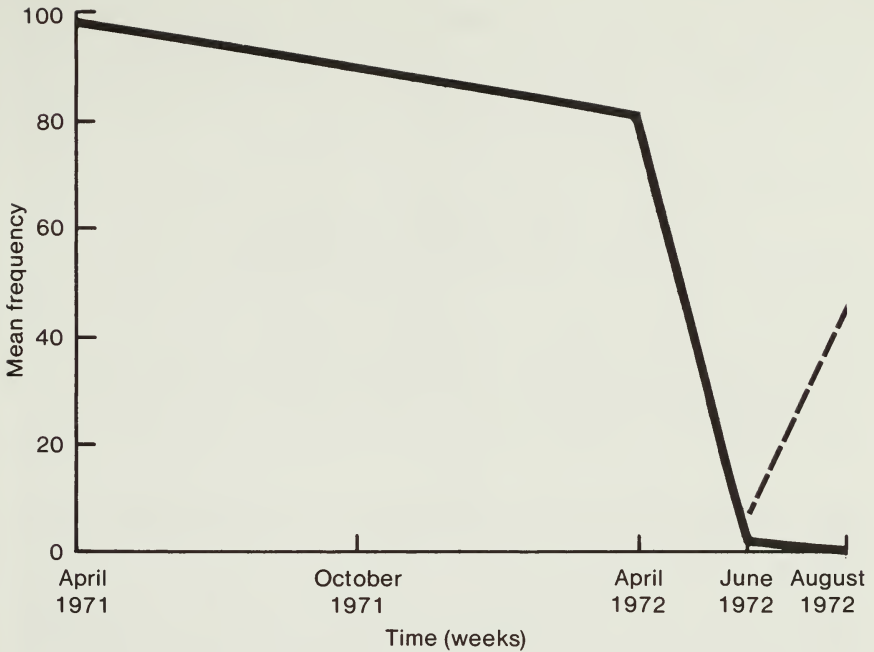


Fig. 3. Comparison of open marsh *Iris pseudacorus* (solid line) and *Peltandra virginica* (broken line) by mean frequency per square meter against time.

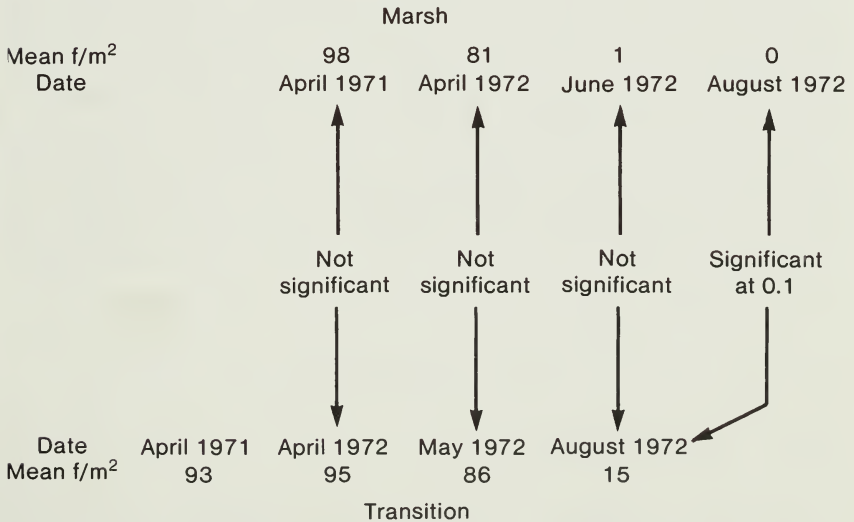


Fig. 4. Comparison of *Iris pseudacorus* decline in swamp-marsh transition with that of the open marsh from data of Tables 46, 42, and 44.

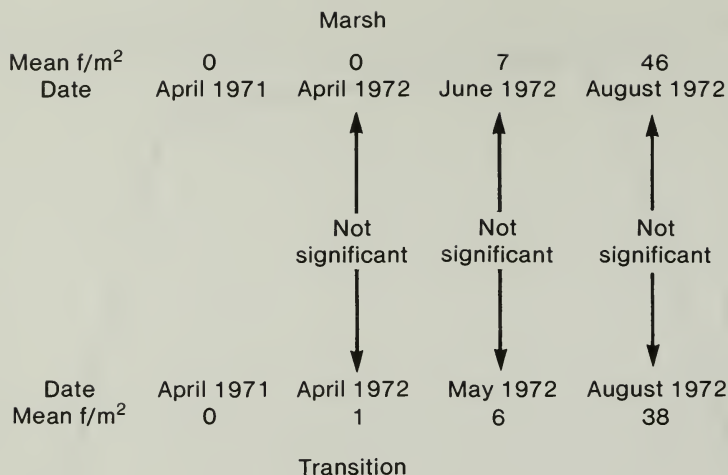


Fig. 5. Comparison of *Peltandra virginica* increase in swamp-marsh transition with that of the open marsh from data of Tables 47, 43, and 45.

species under study. This defunct competition experiment was modified into a germination test with each species being germinated under conditions favorable to itself. As shown in Table 48, *I. pseudacorus* has a low germination percentage (33%) as compared with *P. virginica* (63%). The significance of the difference between these proportions is far beyond the 0.001 level of statistical significance.

Because *Acorus calamus* is in the same vicinity as *I. pseudacorus* plots in the transition area and some *A. calamus* actually invaded some of the control plots, this species was selected to compete against *Iris* in two experiments. With varying proportions of *Acorus* as the treatment, the differences in *Iris* weights are significant at the 0.025 level as shown in Table 49. Thus, in general, the more *Acorus*, the less *Iris* (see Duncan's test, Table 49, for details). The other experiment with varying proportions of *Iris* as the treatment showed the differences in *Acorus* weights were not significant (Table 50); the *Iris* in this case has no significant influence on the *Acorus*.

### Limiting Factors

#### Light as a Limiting Factor

The results of the several surveys which investigated the light differential in different habitats are shown in Tables 51–66. In the forested areas (Tables 51–58), the upland forest without the exotic *Lonicera japonica* or *Hedera helix* receives less light, except in December, Feb-

ruary, March, and June, than those upland areas with these vines. Even in these months, however, this upland forest was still receiving less light than the cleared understory *L. japonica* habitat. This latter habitat consistently receives more light throughout the whole year, including the winter, than the natural understory *L. japonica* habitat. There is no significant difference in light between upland *H. helix* and natural understory *L. japonica* (also on the upland) habitats at any time.

There were no occasions when the flood-plain habitat without *H. helix* received less light than the flood plain with this vine; there were no differences between the two habitats.

The two *Hedera* habitats do not differ in the light received. One might expect, generally, that the upland forest without exotic vines receives somewhat less light than the flood plain without *H. helix*. The data generally support this expectation only from August to November (Tables 51, 52, 58).

In the marsh areas, the surveys showed (Tables 59–66) that there was no real difference in the light received by the different habitats except on 22 December, 30 June, and 22 September (Tables 60, 64, and 66). Note that the differences on these occasions are not clearly related to habitats with and without *Iris*.

Only in the upland area, then, was light indicated to be a limiting factor in the growth of the exotic species that were studied; in the marsh and transition areas, it apparently has little if any influence as a limiting factor. This conclusion was tested in several different ways.

One way of testing light as a limiting factor was by use of regressions. The results of these for *Lonicera japonica* are shown in Table 67. Both regressions are straight line, showing an increase in biomass with increase in light. The regressions when tested were significant beyond the 0.001 level and the coefficient of determination for each shows that light is a very important factor in biomass variation. The results of the *Hedera helix* regressions are shown in Table 68 and the conclusions are similar although it should be noted ( $r^2$ ) that light is not quite as important in explaining biomass variation. In *H. helix*, biomass increase with increase in light is curvilinear.

Light as a limiting factor also was tested by means of controlled shade and light experiments. The results of these are shown in Tables 69–75. The randomized block experiments show that the degree of shade has no influence on the milligrams of chlorophyll per gram of dry-leaf weight (Table 69), which is exactly what would be expected unless the chlorophyll biomass is changing at a different rate than the leaf biomass. Further experiments show that leaf biomass decreases significantly with increase in shade (Tables 70 and 71), thus indicating that in these vines chlorophyll also decreases with increase in shade. Note how well these experiments with leaf biomass support the regression surveys with total biomass (Tables 67 and 68). The experiments show *Lonicera japonica*

decline to be more correlated with shade than is *Hedera helix*; the surveys show *L. japonica* increase to be more correlated with light than is *H. helix*. The experiments with vigor (cover) and shading (Tables 72 and 73) further implicate light as a limiting factor and show again that shade is more important for *L. japonica* than for *H. helix* in limiting growth. The experiments for both of these species also show that biomass is more sensitive to shade than vigor (cover) is. Vigor as explained previously is square centimeters of green or yellow leaves in each square decimeter plot.

An examination of the data of the leaf biomass and the vigor experiments with shade (Tables 70–73) reveals obscurity between some of the treatments. The relative insensitivity of these randomized block experiments was improved by use of regression experiments. The same data were used since the criteria for regression model I had been met in the physical setup for the randomized block design. The results of these reruns are shown in Tables 74 and 75. No conclusion is overturned except for *H. helix* chlorophyll A, otherwise they are all strengthened. Chlorophyll A in *Hedera* changes at a different rate in response to shade than the leaf biomass does.

The results of several other regression experiments are shown in Tables 74 and 75. Since both leaf biomass and vigor are influenced significantly by shade, it might be expected that they would have some correlation with each other, and they do; leaf biomass can be predicted (especially from *H. helix*) from vigor which is easier to measure. Likewise, it would seem that chlorophyll in milligrams per gram of dry-leaf weight is dependent on neither leaf biomass nor vigor (cover) for *Lonicera japonica*, and it is not. But with *H. helix* there would be some correlation, and there is.

Did the cheesecloth actually cut down the light? Light measurements made inside the wire frames show not only that it did but that both sets of experiments were quite uniform; 96% of the variation in the layers of cheesecloth is explained on the basis of light for both *H. helix* (Table 74) and *L. japonica* (Table 75).

The final series of experiments shown in Tables 74 and 75 are with light and they parallel those with shade. They were expected to verify the controlled shade experiments. In all cases except one (*H. helix* total chlorophyll and light), these experiments did verify in varying degrees those with shade. Regardless of this exception, it is shown again that *L. japonica* is more sensitive to light conditions than *H. helix*.

As one final point in the verification of light as a prime factor in abundance of these two exotic species on the upland, note that the survey regression of light and total biomass of *L. japonica* (Table 67) is a straight line and so is the experimental regression for light and leaf biomass (Table 75). *Hedera*, as usual, is not as clear, but notice that both survey and experimental regressions (Tables 68 and 74) are curvilinear.



## Vegetational Strata (Structure) as a Limiting Factor

As mentioned under Vegetational Strata (Structure) as a Limiting Factor in the Materials and Methods chapter, a relationship exists between community vertical structure and light. The experiments with varying degrees of shade and light just described, along with the common observation that it is darker in some forests than in others, indicate such a relationship must exist. The facts shown in the previous section (*Light as a Limiting Factor*) are that light is both a limiting factor for *Lonicera japonica* and *Hedera helix*, and that light differs in habitats that contain these exotics and those that do not. All these facts combined indicate that habitats with and without the exotics should be structurally different.

Table 76 presents the results of the basic data for numbers of vegetational strata. The validity of two herb layers in the forest without exotic vines is also shown.

When the ground layers which contained the exotic vines were compared to similar areas without these vines, it was found (Table 77) that in the flood plain there was no difference in these ground layers but that in the upland there was. These results support the idea of structural change associated with differing amounts of light. Note, for example, that light was not shown to differ on the flood plain (Tables 51–58) and there was no structural difference in ground layer either (Table 77).

The results of comparing the number of strata present at each point in each habitat with the expected number in that habitat (Table 76) are shown in Table 78. Note how these results support strata or vertical structure as a limiting factor. Although the upland forest without exotics shows a significant difference between number of strata at each point and the expected number, the two comparable upland habitats with the exotic vines (upland *Hedera* and natural understory *Lonicera*) show greater significance and show a relatively emptier vertical structure. As was pointed out earlier, the two *Hedera* habitats do not differ in the light which they receive nor do the two flood-plain habitats (Tables 51–58). On this basis, there should be a significant difference between observed and expected structure in these habitats, and there is (Table 78).

Light was not shown to be a factor that differed in the two transition habitats (Tables 59–66) and likewise both transitions show significance between strata occurring at each point and the expected number (Table 78). The swamp, as might be expected, was similar to the transition areas (Table 78).

Now suppose that instead of comparing each habitat with itself as was done and shown in Table 78, that each habitat with an exotic had been compared with its counterpart habitat without the exotic in question. Since in all cases except one the habitat with the exotic has the same number of strata as its nonexotic counterpart (Table 76), the results

would be exactly as shown in Table 78. The one exception is *Lonicera japonica* under the cleared understory. If this habitat were compared with an expected five layers instead of the three layers as shown in Table 78, the significance level would be expected to rise and the vertical structure would become less dense. This is the case. The proportion of strata present dropped to 0.360 and pooled chi-square rose to 20.48 which is significant beyond 0.001.

When each stratum was compared to every other stratum in all combinations in each of the nine habitats shown in Table 78, the results showed no correlation of any layer with any other except in the swamp-marsh transition without the exotic *Iris pseudacorus*. In this one habitat, the null hypothesis that the low herb stratum is independent of the understory stratum is rejected at 0.07 (exact); the tetrachoric coefficient of correlation is about +1.0. In this same habitat, the comparison of the tall herb layer with the understory resulted in a relatively high tetrachoric coefficient of +0.57 but the chi-square was not significant at the 0.1 level. The comparable habitat with *I. pseudacorus* yielded no such differences in structural relationships, although a tetrachoric coefficient of +0.55 occurred with the comparison of the low herb stratum with the tall herb stratum; chi-square, however, was not significant at the 0.1 level. (*I. pseudacorus* is in the tall herb layer.)

The results of combining the data showed mostly no significance and low tetrachoric coefficients. Those that were significant, i.e., that showed dependence of one layer with another, are shown in Table 79.

The qualitative test of association of layers indicates that structural differences along these lines between exotic and nonexotic areas exist only in the swamp-marsh transition where light apparently plays only a small part, if any, in limiting *Iris* growth.

The positive results with the swamp-marsh transition area together with the results shown in Table 79 indicated that there might yet be, as a general rule, structural differences of layer associations between areas with and without exotics. This led to quantifying these relationships by regressions. As mentioned under this corresponding section in Materials and Methods, only the three woody layers were measured; however, they must all compete with the herb layers where the exotic is.

The results of the multiple regressions were disappointing in that only a single one of the eight, flood-plain *Hedera* (cleared understory *Lonicera* was not done as previously explained), was significant. It was significant at the 0.01 level and has a very high coefficient of multiple determination ( $R^2_{1,23}$ ) of 0.849, which means that 85% of the variation in depth of the shrub layer is explained by referring to depth of both overstory and understory. One coefficient of partial determination ( $r^2_{13,2}$ ) is 0.572 which means that overstory depth has explained 57% of the variation in shrub depth that understory depth has failed to do. The other coefficient of partial determination ( $r^2_{12,3}$ ) is 0.796 which means that understory depth

has explained 80% of the variation in shrub depth that overstory depth has failed to explain.

Perhaps the multiple regressions were obscuring some of the relationships. Simple linear regressions were run and most of them were not significant. Those that were significant are shown in Table 80 along with nonsignificant regressions of similar habitats for comparison. (The nonsignificant regressions of the swamp and the swamp-marsh transitions, both with and without exotics, are not shown.) Note that the only significant correlations were with *Hedera helix* habitats and the coefficient of determination is high also. There were no significant correlations with the counterpart habitats without *H. helix*. Thus it appears that for *H. helix* there is a structural difference (layer association) between exotic and nonexotic areas other than that shown in Table 78. Note also that the two *Hedera* habitats (Tables 51–58) did not differ any time with the amount of light received.

Can two vegetation types (or microtypes) be discriminated on the basis of foliage depth of overstory, understory, and shrub layers? The results of discriminant function analyses are shown in Table 81. The answer is “yes” to four of the seven comparisons, and this is with the no exotic forest and cleared understory *Lonicera* in which light is a big environmental difference (Tables 51–58) and the swamp-marsh transition areas in which light was not a big factor in the habitats (Tables 59–66). [Because the shrub layer is missing in one of these transition habitats and the understory is missing in the other (Table 76), the two layers were combined into a shrub-understory layer for the analysis.] However statistically insignificant the discriminant function is for the other comparisons, there appears to be a biological significance which is verified a number of times. Note the comparison of the upland forest without exotics with the upland *Hedera helix* that the overstory is the least valuable for discriminating between the two types; that is, the overstory in the nonexotic and exotic areas are similar. Conversely, the shrub layer exhibits the greatest difference between the habitats with the understory being intermediate. Note that the same pattern is repeated for the other two upland habitat comparisons (*Lonicera japonica*).

Because the results (particularly Tables 77, 78, and 80) show there are structural differences between areas with and without *H. helix* and *L. japonica*, the surveys to investigate *Ulmus americana* depopulation and its relation with these exotic vines were taken.

The results of the first *U. americana* survey show (Table 82), for exotic vines in general and *H. helix* in particular, that these overstory trees are about equally infested or free.

Analysis of cross-classified data in analytical tables is likely to be unfamiliar to many biologists; therefore the results (Tables 83–88) will be described in more detail. Cross-classification is a way of analyzing discrete variables from a survey in such a way that one or more can be



held constant while varying another. In this way, it is similar to multiple (partial) regression which is used for analyzing continuous or measurement variables.

The results of censusing nonvigorous, standing overstory trees and exotic vine infestation are shown in Tables 83 and 84. Note from Table 83 the fact that *Ulmus* without exotic vines (35%) and all other trees without exotic vines (58%) are not near the overall average of 51%. Conversely, *Ulmus* with exotic vines (65%) and all other trees with exotic vines (42%) are not near the average of 49%. This indicates that these exotic vines are associated more with nonvigorous, standing overstory *Ulmus americana* than all other nonvigorous, standing overstory species combined. In like manner, Table 83 shows an association of *Hedera helix* with the nonvigorous, standing overstory *Ulmus americana*, but the other differences (*Lonicera japonica* and both species on the same tree) are so near the overall average that the relationship is obscured. These results are clarified by considering the third variable, vigor of tree. The significant differences are shown in Table 84; Table 83 shows which percentages (for *Ulmus* or others) are greater. Now, by holding dead trees constant, the data show exotic vines significantly associated with *Ulmus*. Specifically, it is *H. helix* that is so associated, for the data show *L. japonica* is not significantly associated with dead *Ulmus*. Examination of the "dying" variable shows that *L. japonica* is significantly associated with dying *U. americana*. Thus, exotic vines are significantly associated with nonvigorous *U. americana* in the following manner: *H. helix* is associated with dead trees and *L. japonica* is associated with dying trees. Note that the more light-sensitive (see *Light as a Limiting Factor* section) *L. japonica* behaves as expected when more light is allowed in because of a dying crown. Now, if the tree types are held constant (read down the columns, in Table 83) little variation can be noted between dead and dying categories for "All others," but for *U. americana* there is relatively more.

The results of censusing fallen overstory trees and exotic vine infestation are shown in Tables 85–88. Table 86 presents the necessary data for analyzing the two variables of tree type and exotic vine status, and Tables 87 and 88 present the necessary information when the third variable, type of fall, is included in the analysis. In the two-variable analysis, note that down *Ulmus* trees are associated more with exotic vines than all other species combined. The three-variable analysis gives the details. The data show that with a natural tree fall, *Hedera helix* is significantly associated with *Ulmus*, not other species, before the fall. This follows from the previous survey which showed *H. helix* significantly associated with dead *U. americana*. With a natural fall, this vine is associated more with other species after the fall. Compare this with the previous survey which shows no significant association of *H. helix* with other species.



*Lonicera* occurrence before a natural fall is significantly associated with *Ulmus*, which also supports the results of the previous survey which showed both these exotic vines as significantly associated with *U. americana*. The data in these tables (Tables 85–88) also show that with either *H. helix* or *L. japonica* occurring both before and after a natural fall, there is a significant association with *U. americana* but not with other species. In cut falls, the exotic vines are mostly on *U. americana*, while other species are significantly associated with the free condition. One exception is that *L. japonica* occurrence before the cut is significantly associated with other species. Most of the data show that in a cut fall, the exotic vines which associate with *U. americana* are *H. helix*. This vine is significantly associated with *U. americana* after the cut. The data also show the significant association of *H. helix* with *Ulmus* before as well as after a cut fall. Note that many of the “within group” differences (differences between natural and cut fall within each column of Table 85) are not as great as the between-group differences (Table 88). The biggest difference is under *U. americana* in the *Hedera* after fall column (Table 85) where there is a large difference between cut and natural fall (32 and 15%, respectively).

This final survey (*U. americana* and down trees) verifies structure as being a limiting factor in exotic vine growth, particularly with *H. helix*.

#### Duration of Water Inundation as a Limiting Factor for *Iris*

As pointed out earlier, when mention was made that the defunct competition experiment between *Peltandra virginica* and *Iris pseudacorus* had to be modified to germination tests, lengthy water inundation apparently inhibits *Iris* growth. As mentioned in Materials and Methods, an indirect way to measure length of inundation is by determining the topographic slope. The results of this determination are shown in Fig. 6 and Table 89. One point appears out of place in Fig. 6 but the data in Table 89 show a significant slope from the tree line or forest edge (swamp-marsh transition) down to the bank of the gut. Since the *I. pseudacorus* in the swamp-marsh transition, as mentioned earlier (*Control Check*, Materials and Methods), was not dying out as fast as that in the open marsh, the presence of this slope verified the length of inundation hypothesis. Note (Table 89) that there is no slope of the marsh from head to mouth. There would, of course, be a slope of the gut channel but this was not measured.

The results of measuring the elevation on each *Iris* control plot and similar areas without *Iris* are shown in Table 90. Note that this verifies again that *I. pseudacorus* areas are at a higher elevation than their non-*Iris* counterparts, thus they are inundated for a shorter period of time by the tides.

As pointed out under Light as a Limiting Factor (Results), light is apparently not a limiting factor in *I. pseudacorus* growth in the open marsh and swamp-marsh transition areas. The result of the multiple regression that compared both light and topographic slope to *Iris* biomass is shown in Table 91. Note that the equation is a significant representation of the relationships involved, but as the partial correlation shows, the use of light is not warranted. Thus, that light is not a limiting factor for *I. pseudacorus* is verified along with verification that topographic slope is important. With light eliminated from the regression (simple regression), statistical significance increases. Note that while biomass increases with elevation, it decreases with light (i.e., it increases with shade). The coefficient of determination for the simple regression with light, however, was only 28%.

The coefficient of determination for *Iris pseudacorus* biomass and elevation was 47%, which means that 47% of the variation in biomass is explained on the basis of elevation. This leaves 53% of that variation unexplained. Three other factors (other than light) were investigated: vegetation, soil color, soil hardpan.

The analysis showed that the vegetation was a *Peltandra virginica* zone and exhibited no significant differences in the presence of this species in *Iris* and non-*Iris* areas (Table 92).

Table 93 shows that, for the soil color investigations, *Iris pseudacorus* in the transition area is significantly associated with gley soil. This is opposite to expectations. Less gley would be expected at the higher elevations where oxidation can take place.

The results of the hardpan studies (Table 94) seem to explain the expectation reversal because the *Iris*, particularly in the transition, is significantly associated with a hardpan which, of course, would tend to exclude oxygen (Lutz and Chandler 1946:258, 259) regardless of elevation.

Thus, of the factors investigated, length of water inundation appears best as a limiting factor. One final test of this hypothesis was made. If this hypothesis is correct, then the amount of water in the Potomac River during the growing season must have increased in recent years. Table 95 shows that this, in fact, is what has happened.

### *Miscellaneous Observations*

Table 96 shows several helpful miscellaneous observations. Note that the mature *Iris* growing on gravel above or at the limit of high tide supports the hypothesis of the length of water inundation as a limiting factor for that species. Attention is also called to the fact that the *Iris-Acorus* competition experiments support the observation recorded in Table 96 that *A. calamus* can take over *I. pseudacorus* sites.

## *Evaluation of Methods for Abundance*

In both the surveys for exotic plant dominance and the experiments for rate of exotic plant growth, abundance was determined three ways: frequency, cover, biomass. Biomass takes the longest time to determine and frequency takes the shortest time. Table 97 was compiled from several tables as indicated; it shows the comparability of results of the different methods.

Frequency could be used as a rough estimate of cover, and cover can be used as a rough estimate of biomass, but frequency is no estimate of biomass. Kershaw discusses (1966:17, 18) some of the problems one finds in using frequency as a measure of abundance. Both the effect of plant size and spatial distribution (pattern) which he discusses would enter into explaining the nonconcordance found in my use of these methods. When the same species (*Hedera helix*) is dealt with, the problems presented by Kershaw are mitigated and frequency becomes a little more comparable with biomass, but still not enough to build any confidence in its use. The concordance between frequency and cover found in checking the *H. helix* controls (Materials and Methods) was due to the fact that most of the squares in the grid were filled, so that cover was actually or virtually equal to frequency. The data summarized in Table 97 show that even with some discrepancy between frequency and cover, that frequency is often a rough estimate of cover.

If the significance level for cover (Table 4) had been set at the 0.05 level, then concordance of cover and biomass would be even better than it now is (Table 2). The cover and biomass referred to thus far is total cover and biomass. The controlled shade experiments (Tables 74, 75) show that leaf biomass can be predicted to some degree, depending on the species, from leaf cover (vigor) by a straight line equation. This is further indication of the close relationship of cover, which is an indication of size or volume, and biomass, which is a measure of nutrient removal.

In conclusion, when frequency on a grid closely approaches cover on an area basis, it will provide results of abundance similar to biomass (since biomass can be estimated from cover). Because of the size and pattern factors, frequency is more likely to approach biomass with a given species (or a very closely similar one in size and growth form) in the same habitat (or one that allows a similar spatial pattern to develop). As long as frequency remains only a very rough estimate of cover, it cannot give the same results of abundance as biomass.





The author (right) and his assistant, Michael J. Blymyer, working in an upland *Hedera helix* block.



## Discussion

### *Lonicera japonica*

It appears that the impact of *Lonicera japonica* upon the indigenous vegetation of Theodore Roosevelt Island is to destroy the forest, and the key to this destruction is the amount of light that reaches the forest floor.

From general observations of the past (qualitative survey, if you will) both on and off the island, it would appear that *L. japonica* does not do well in the shade. Similar observations have been made and similar conclusions have been drawn by other observers including Leatherman (1955:26, 27, 58). Everyone has a hunch, but there is a dearth of data. Good quantitative data to support this hypothesis are lacking in the literature. Leatherman's study comes closest and a review and commentary on that study will be instructive. Leatherman transplanted 10 cuttings to each of three different habitats (open, deciduous forest, evergreen forest) at each of four elevations (Leatherman 1955:19-21). After 3 months, a comparison was made; the best growth and cutting survival occurred in the open habitats (at 6000 ft and 5200 ft), but the poorest growth and survival also occurred in open habitats (at 3500 ft and 1500 ft). Slight differences in shoot-root ratios (dry-weight basis) of *L. japonica* in the different habitats were not statistically significant (Leatherman 1955:21). These habitats were described (Leatherman 1955:22, 23) but the description of light intensity was taken from a measurement on only one day. In studying the development of the seedling, Leatherman (1955:40, 43, 44) grew 10 plants each in the greenhouse; full sun, 25% of full sun, and 5% of full sun. The average weight (in mg) of the combined shoots and roots is 0.4 mg higher in the 25% of full sun than in full sun (Leatherman 1955:43; my calculation from Leatherman's data). The 5% of full sun was 9.5 mg lower than the 25% of full sun (my calculation). The average length of shoot, however, did decrease with full sun, while the average length of root increased. From colonies of mature *Lonicera japonica*, Leatherman (1955:47) found the average weight of 100 sun leaves to be 0.063 g, while that of shade leaves was 0.031 g. Three photosynthesis measurements were also made on leaves

by using a modification of the matched-leaf method of Denny: potted plants, cuttings, and intact plants (colonies) (Leatherman 1955:48, 49). In each case, the dry-weight increase in full sun and 25% of full sun was determined, and for the cuttings the dry-weight increase for 5% of full sun was also determined. The percent of dry-weight increase was greatest in full sun and least in 5% of full sun; this was significant at the 5% level (Leatherman 1955:49, 50). Full-sun leaves consistently showed greater weight than the 25% of full-sun leaves; however, the differences were not statistically significant (Leatherman 1955:49, 50). In another study of light, Leatherman (1955:50–53) placed 10 cuttings each in five plots near the greenhouse; varying layers of cheesecloth were placed over four of the plots. The experiment lasted 160 days. Actually, more plants survived under 50% and 25% of full sun than under full sun. The number of nodes per plant decreased with decrease in light. The combined average dry weight of shoots and roots declined consistently from full sun to 5% of full sun.

Thus, it would appear that there are some quantitative data which are not altogether consistent in their support of light as a limiting-factor hypothesis for *Lonicera japonica* in the deciduous forest. By using intact plants already and long established in the habitat, I avoided the variation that would be associated with survival of cuttings. Instead of taking only one light measurement in a habitat, I replicated the measurements both by location and time in each habitat. In addition, I replicated my cheesecloth-shading experiments.

The sequence of events that leads to forest destruction by *L. japonica* appears to be as follows. To begin with, some disturbance of the vertical structure of the forest must occur, for *L. japonica* areas have a different proportion of the vertical layers present than the nonexotic forest (Table 78; also Tables 76, 77). It is not necessary that the overstory be removed to bring about this change (Table 81). The *Acer negundo* which was removed from Little Island with subsequent invasion by *L. japonica* was probably understory. As shown in Table 81, it is the shrub layer which is the most variable between the *Lonicera* areas and the forest without exotics.

The disturbance of the vertical structure allows more light to come into the forest. This is shown by increased light in the *L. japonica* areas compared with the forest without exotics (Tables 51 through 58). (Recall that both vertical structure and light intensity were studied at the same stations.) In the winter (December, February, March) the least-disturbed *L. japonica* areas have similar light intensities to the forest without exotics. This is a time when *Quercus* spp. and *Fagus grandifolia* (beech) would be expected to have fewest leaves. The only other time of similar light intensities is in June.

The more light, the heavier the growth of *Lonicera japonica* (Tables 67, 75). This light-stimulated growth is in the form of cover (vigor) as

well as biomass (Table 75). With changing degrees of shade, the biomass of chlorophyll does not change at a rate different from that for leaf biomass as a whole. Growth may be slightly faster on a new area than on an area already established with *L. japonica* due to less competition.

In a forest which is less disturbed, this growth of *L. japonica* on the forest floor suppresses the normal ground layer and replaces it with another ground layer. The new ground layer is, in a sense, not a replacement but an additional layer formed at a lower height than the original (Table 77). In a badly disturbed forest, the *L. japonica* becomes vigorous enough to stand at the same height as the original ground layer (Table 77).

This differential growth is reflected in the amount of biomass produced (Tables 2, 6), with significantly more being produced in the habitat with the greater vertical-structure disturbance. In the slightly disturbed area, growth of *Lonicera japonica* is relatively slow, with no significant difference between the biomass growth of 1 year and that of 1.25 years (Table 5). Frequency as a substitute for cover reflects the same growth rate (Tables 9, 10). In a more disturbed area, production of biomass is more rapid (Table 5). By using frequency as an indication of cover, it will be seen that in highly disturbed areas 90 days after removal, *L. japonica* will appear as though it had not been removed (Table 15). Cover recovery is not so rapid in areas disturbed only slightly (Tables 10, 17); however, after 1.25 years, recovery may approach the original condition (Table 10).

Some of the impact has been alluded to in the suppression of the ground layer. Since plants of all forest layers must pass through this ground layer in their growth, suppression in this layer will promote far-reaching structural changes over a period of generations. Life form or growth form is not synonymous with vegetational stratum, but there is a relationship between the two because of the usual heights attained by the different growth forms.

In mildly disturbed forests, *Lonicera japonica* suppresses trees, particularly *Prunus serotina*, and other woody plants, especially *Parthenocissus quinquefolia* (Table 30). The data show no significant difference between the impact of *L. japonica* on herbs and on woody plants (Tables 30, 31). The anomalous herb data of Table 30 are very close to meeting the statistical significance level.

When the forest is highly disturbed, suppression becomes more marked (Table 35). Although herbs in general and *Oxalis stricta* in particular are suppressed by this exotic vine, one species, *Allium vineale*, is not so affected. Apparently, the long, narrow leaves of this exotic herb which poke up through the *Lonicera japonica* get sufficient light and nutrients to remain unaffected by the presence of the vine. Herbs are more abundant in open areas than in forests and the highly disturbed forest is like an open area. This explains the greater suppression of herbs

here than in the mildly disturbed forest (Table 38), although the suppression is not statistically significant.

The only species which occurred frequently enough in both the mildly and highly disturbed forests to permit analysis was *Parthenocissus quinquefolia*. This woody vine was suppressed more in the mildly disturbed habitat than in the highly disturbed habitat (Tables 30, 35, 37). The nontree, woody plants as a group are not suppressed in this highly disturbed area (Table 35); these are mostly woody vines, not shrubs. Under more natural conditions, these vines receive sunlight in the tops of the trees. In this highly disturbed habitat, they receive the light on the ground (Tables 51–58). Regardless of the degree of disturbance, *Lonicera japonica* definitely suppresses trees (Tables 30, 35). In the highly disturbed forest, *Liriodendron tulipifera* and *Ulmus americana* were particularly affected. These results agree with the report of Little and Somes who say (1967:1) that the vine is particularly luxuriant in openings and usually prevents reproduction of other vegetation. However, they present no data in support of their statement.

The impact of *Lonicera japonica* in a highly disturbed forest is apparently not different in kind from that of a mildly disturbed forest (Tables 38–41). Therefore, the impact of this exotic vine in the highly disturbed forest is merely a magnification or speeded-up process of the same impact on a mildly disturbed forest. The three tree species (*Ulmus americana*, *Prunus serotina*, *Liriodendron tulipifera*) which are most adversely affected by *L. japonica* are among the dominants of the island upland (see Introduction). With reproduction in all potential layers suppressed, the vertical structure will become more open or empty as the mature vegetation dies. This will allow more light to come in and speed up the growth of *L. japonica*, which will hasten the demise of the forest. At the same time that the forest is dying, the species composition will change because all species are not affected at the same rate. At present, the forest is slowly headed toward one without *U. americana*, *P. serotina*, and *L. tulipifera* as principal dominants.

If the present infestation on healthy trees were the same as on dying trees and this in turn were the same as on dead standing trees and likewise on dead down trees, it would be assumed that the infestation was stabilized. The principal present overstory dominant, *Ulmus americana*, is relatively free of *Lonicera japonica* (Table 82). The low infestation associated with dead standing *Ulmus* is approximately the same as that of all other dead standing overstory trees (Table 83). The dying trees other than *Ulmus* have essentially the same infestation level as the dead trees, but *Ulmus* has significantly more *L. japonica* than other dying overstory trees (Tables 83, 84). Something has stimulated *L. japonica* in the recent past to grow on more trees of *U. americana*. The sequence appears to be as follows. In 1963, during the time when observations were being made for the dendrological survey and floral checklist, several



*Ulmus* (approximately 50–73 cm diameter, 17–75 cm above soil line) were cut ostensibly for control of Dutch elm disease. However, neither trees nor bark were removed from the island. This increased the breeding habitat for the inner-bark boring beetle *Scolytus multistriatus* (Marsh.), the smaller European engraver (Anderson 1964:239; Welch and Matthyse 1960:4, 5, 9; Boyce 1948:299). I have not seen the galleries of the native elm bark beetle *Hylurgopinus rufipes* (Eich.) on the island. Both fungus and beetle build up in these dead logs (Matthyse 1959:2, 6, 9). It usually takes a large number of feeding marks by the beetles to cause infection (Matthyse 1959:10). With an increased population of both fungus and beetle, more *Ulmus* would have the disease. By 1965, the incidence of the disease on Theodore Roosevelt Island reached the point that plant pathologist Horace V. Wester (National Park Service) recommended an active sanitation program, but such a program was not carried out (Chick 1966). As the trees die from the disease, the crowns open up and allow more light to enter the forest. *Lonicera* is very responsive to light (Table 75), especially when invading an area (Table 67). Thus, the proportion of *U. americana* trees with *L. japonica* on them increases over the standing dead trees which represent the infestation of a previous generation of living trees (Table 83). At the same time that the exotic vine was stimulated to grow on an increasing proportion of dying *U. americana*, the surrounding vegetation was also stimulated and the crowns of the nearby trees expanded. The beetles can breed only in tight-barked wood (Welch and Matthyse 1960: 6, 9). By October 1972, there was already no breeding habitat on the down trees (Table 96). With the beetle population down, the death rate of *Ulmus* decreased and hence the invasion rate by *L. japonica* would also decrease so that the present proportion of infestation on the current generation of healthy trees has decreased (Tables 82, 83). But it is not down to the 8 or 9% found on dead standing trees (Tables 83, 84), which is greater than the 3% growing on trees before they fell (Table 85). Overall, the conditions for growth of *L. japonica* have improved over the years.

The growth of *Lonicera japonica* on overstory elms serves to some extent as an indicator of the vigor of the tree, but, except for some root competition, probably does not affect that vigor. Reports of *L. japonica* overwhelming vegetation (Whipple and Moeck 1968:1; Little and Somes 1967:1; Penfound 1966:190, 191; Gunning 1964; Oosting 1956:208; Leatherman 1955:26, 27, 84, 86; Kephart 1939:1; Handley 1945:263) are with less than usual-sized overstory trees. Daubenmire (1965:304, 305) points out that woody twiners constrict the host stem and subsequently interfere with downward translocation in the host and the host tissue overgrows the liana with apparently similar results. Leatherman also suggests (1955:26, 27) that death or impaired growth of trees was due to interruption of translocation of food to the roots by *L. japonica*.

Most overstory-sized trees escape this kind of death or impairment. Since vines have a weak stem, twiners apparently need branches or stubs for support as they climb. Honeysuckle stems may elongate up to about 1.5 m in a growing season (Leatherman 1955:45, 68). On relatively low-growing vegetation, there are many small branches on the trunks for the vine to rest upon. Large trees have no such supports unless another vine with branches is already on the tree. *Lonicera* could not grow up with the tree and thus have its leaves in the forest overstory like *Vitis* spp. because it overwhelms and suppresses small trees. When an overstory tree falls, whether it falls naturally or is cut, the opened canopy with increased light promotes the growth of the vine (Table 85).

Honeysuckle is able to outcompete the native deciduous vegetation in the lower stratal layers (and hence eventually the upper stratal layers) apparently because it is evergreen in this area (see also Leatherman 1955:46) and grows when the native vegetation is leafless. Leatherman says (1955:26) that *Lonicera japonica* growth begins before deciduous trees produce leaves. In Tennessee, it was noted (Leatherman 1955:46) that growth began (in 1953) during the middle of January. In a New Jersey forest, growth began when the temperature was between 1.1° C and 8.9° C (34 and 48° F) (Leatherman 1955:45). The end result is that once *L. japonica* gets started in an area such as this island where climate, soil, and prairie sod are not limiting factors (see Leatherman 1955:30, 32), it creates and promotes its own best environment, and the forest is ultimately doomed. Leatherman reports (1955:62) that this species blooms profusely in full sun with a heavy production of fruit; therefore, as the forest opens up not only is vegetative growth increased but so is seed production. The potential germination percentage of these is about 85%, while the actual percentage is 63% (Leatherman 1955:63, 38). Penfound describes (1966:189) two treeless, vine-dominated communities: one dominated by *Vitis* spp. on an island and the other dominated by *Ampelopsis arborea* (pepper vine) and *Smilax bona-nox* (bullbrier). Without some other limiting factor, the final result on the disturbed forest areas of Theodore Roosevelt Island may well be a similar treeless community dominated by *Lonicera japonica*. That other limiting factor may be *Hedera helix*.

This vine (*L. japonica*) is not reported as a pest in Japan (Leatherman 1955:29, 64) and there appear to be two possible reasons for this. In a climatic analysis which involved only one Japanese station, the type locality of Nagasaki, Leatherman learned (1955:17, 79) that it receives more rainfall (and has a mesothermal rain-forest climate) than areas in the United States where *L. japonica* is a pest. Secondly, the common horticultural variety in the United States is *L. japonica* var. *halliana* (Dipp.) Nichols. (Leatherman 1955:4) which is a more vigorous variant than other members of the species (Leatherman 1955:5). In Japan, the common variety is apparently *L. japonica* var. *repens* (Sieb.) Rehd.

(Leatherman 1955:15). Through evolution, Japanese forests probably have been selected for resistance to the vine which is confined to its niche.

### *Hedera helix*

The impact of *Hedera helix* on the forests of Theodore Roosevelt Island is similar to that of *Lonicera japonica* in that it destroys the forest.

From general observations on the island, it appeared that light was a limiting factor for *H. helix* (as well as for *L. japonica*). Grasovsky (1929:49, 25–27), however, believes, after investigating several species including *H. helix*, that the effect of light in the forest has been overrated. Grasovsky's study (1929:28, 30, 31–35, 37–39, 40, 41) is the only one found that deals with light as it relates to this exotic vine. A brief review of this investigation as it relates to *H. helix* will be instructive. The experiment concerning this species consisted of a box fitted with a glass window at one end through which daylight passed. Cuttings of *H. helix* were placed in pots and two plants were placed at each of four distances from the window. The box was ventilated to control the temperature. Hourly measurements of light were taken on all clear days in the summer for the 10-month experiment. At the end of the experiment, the *Hedera helix* receiving a maximum illumination of 10,000 foot candles (ft-c) and 280 ft-c were in vigorous condition, while those receiving 65 ft-c were in good condition, and those receiving 25 ft-c were in poor condition. If 10,000 ft-c are considered full sunlight, then 280 ft-c are approximately 3% of full sunlight (Grasovsky 1929:35). In like manner, 65 ft-c and 25 ft-c are about 1% and 0%, respectively. Although those at 65 ft-c were considered in good condition, they were dying. The dry weights of the plants (all species studied) at the end of the experiment were too variable to support the conclusion of more biomass associated with more light; *Hedera* dry weights are not mentioned specifically. This experiment was apparently not replicated and the potted plants apparently were not weighed before the experiment. Grasovsky also took hourly light measurements at frequent intervals during the growing season on two plots under white pine; the forest floor was covered with pine needles or had a scanty vegetation. Since the light in these pine stands sometimes exceeded the minimum light requirement as found by Grasovsky in previous experiments, he concluded that light was not the limiting factor. On the basis of Toumey's trenched-plot experiments in the same plots, Grasovsky concludes that soil moisture is the factor limiting growth under the pines.

The quantitative data for or against light as a limiting factor for *Hedera helix* growth in the forest seemed inadequate. I used intact plants already established in the habitat and replicated both my survey observations



(in time and space) and my experiments. In addition, the  $1 \times 1\text{-m}$  plots were trenched to nullify the moisture factor. According to Grasovsky's study, *H. helix* ought to do well at 3% of full sunlight and the critical point would be somewhere between 3% and 1%. This means that all the forest areas on the island that are presently without *H. helix* are available habitat waiting for invasion (Tables 51–58) because they all receive much more than 3% of full sunlight. My controlled light experiment with cover (vigor) comes closest to Grasovsky's experiment and it shows (Table 74) that with an increase in shade or decrease in light the condition of *H. helix* will decline. The situation is more apparent when leaf biomass rather than vigor (cover) is considered (Table 74). For example, some raw data (part of which enters the vigor and light equation of Table 74) show that between 4 and 7% of full sunlight was associated with 25–58  $\text{cm}^2/\text{dm}^2$  of *H. helix*, while 65 to 68% of full sunlight was associated with 100  $\text{cm}^2/\text{dm}^2$  of *H. helix*.

It should be evident that the greatest single factor that accounts for *Hedera helix* growth on the island upland is the amount of sunlight (Table 74; note the coefficient of determination). It is equally evident that light is not as much of a factor in *H. helix* growth as it is in *Lonicera japonica* growth. Compare the coefficient of determination for significant regressions of Table 67 with Table 68 and Table 74 with Table 75. There is some other important factor(s) operating. Lack of moisture is probably not the factor limiting the spread of *H. helix* since its growth in the more moist flood plain was slower than on the upland of the island (Table 6), and yet the light relations of both *Hedera* habitats were not significantly different (Tables 51–58).

The events that lead to forest destruction by *H. helix* appear to be similar in some respects to those associated with *L. japonica*. As with *L. japonica*, some disturbance of the vertical structure of the forest must occur on the upland areas, for *H. helix* areas have a different proportion of the vertical layers present than the nonexotic, upland forest (Tables 78, 81; also Table 77). Vertical-structure disturbance allows more light to come into the forest (Tables 51–58). About half the year, mostly in winter and spring, the *H. helix* upland areas have light intensities similar to the upland forest without exotics.

The situation on the flood plain is different. The flood plain without exotics is normally more open or vertically empty than the island upland forest without exotics (Table 78) and allows more light to enter (Tables 51–58), for about  $\frac{3}{8}$  of the year (mostly summer and fall). As might be expected, then, the vertical structures on the flood plain with and without *Hedera helix* are not only similar to each other but similar to the upland areas with *H. helix* (Tables 77, 78), and the light relations of these three habitats are not significantly different either (Tables 51–58). This does not necessarily mean that the vertical structure on the flood plain is in itself conducive to *H. helix* invasion without disturbance. The flood



plain is not only structurally different from the island upland forest (see also Table 81), but the flood plains with and without exotics are different (Table 80).

There is a peculiarity of vertical structure associated with *H. helix*, whether on the island upland or on the flood plain, in that some strata are correlated with other strata (Table 80). This correlation does not occur in the other areas studied, exotic or otherwise. On a qualitative basis, this type of correlation began to emerge only when large numbers of observations were made (Table 79).

As pointed out earlier in this discussion, light is an important factor in the growth of *Hedera helix* on the island. The more light, the heavier the growth of mature or established *H. helix* (Table 68). The light-stimulated growth influences biomass to a greater extent than cover (vigor, Table 74). Light is less of a factor in growth when *H. helix* is invading an area (Table 68). Only 41% of the variation in total biomass is explained by referring to percent of open sunlight.

In the disturbed upland forest, *H. helix* suppresses the normal ground layer and in a sense forms an additional layer at a lower height than the original (Table 77). To this extent, *H. helix* acts like *Lonicera japonica*. But on the flood plain, the ground layer is merely replaced compositionally.

In either case, flood plain or island upland, the differential biomass growth due to sunlight is not significantly different in one habitat over another (Table 2). There may be a slight difference in cover between the two habitats (Table 4), with the upland having the greater cover. The rate at which both cover and biomass is produced does differ (Tables 5, 19). English ivy grows faster on the island upland (Tables 6, 21). One factor which slows the growth on the flood plain is apparently a high water table; no *Hedera helix* was found growing in the swamp (Table 96) which is often only a few centimeters lower than the flood plain.

Kassas (1952:50, 58, 59, 61) found the same result in studying drainage factors in a fen: *H. helix* is limited by waterlogging of the soil, and Mittmeyer (1931:367) calls this species a xerophyte. Another related factor is flooding itself, which is not only a more severe case of high water table but is accompanied by hydraulic force against the plants. This slows the rate of growth even more (Tables 5, 7, 22; the 1.25 years' data were taken after the flood of Hurricane Agnes).

The flood of Hurricane Agnes (June 1972), although unusually severe in volume (Table 23), would not be different in kind from lesser more frequent floods. *Hedera* and other ground-cover plants associated with it have no influence on how much mud is deposited in big floods (Tables 24, 23). A combination of mud deposition and water force removed all vegetation to a significant degree from square meter plots. The *H. helix* was more vulnerable than the native flood-plain vegetation (Tables 25, 26, 27).

*Hedera*, regardless of habitat, suppresses herbs (Tables 28, 33), but

it suppresses them more on the upland (which explains the dearth of wild flowers) than on the flood plain (Tables 28, 33, 38). Reproduction of woody plants in general and trees and other woody plants in particular apparently are not suppressed in either habitat, except for a possibility on the upland (Tables 28, 29, 33, 34, 39, 40, 41). Some data for the upland (Table 28) indicate suppression of nontree, woody plants and possibly trees (the latter group just misses significance), but the other data cited do not necessarily support this suppression. Apparently, the suppression, if it exists on the upland, is subtle and a larger sample would be required for it to be revealed. In any case, herb suppression is greater than woody-plant suppression regardless of habitat (Tables 28, 29, 33, 34).

On the flood plain, the impact of *Hedera helix* on the herbs appears to be about the same as the impact of the flood of a large hurricane (Tables 27, 33); the impact of the exotic vine on upland herbs exceeds this (Table 38). The woody plants of the ground layer, although affected as much as the herbs by the big flood (Table 27), appear not to be affected at all by flood-plain *Hedera* vegetation (Table 33). At ground level, there is apparently no competition between *H. helix* and other woody plants on the flood plain: possibly the same may be said for the island upland (Table 28). But as was previously pointed out, the data are not entirely clear whether *H. helix* impact is the same on both upland and flood plain of the island. If it now is assumed that there is a slight but real difference in the impact between these two habitats, then there is a theoretical explanation, at least in part. As was brought out in the discussion of light and vertical structure, the flood plain is more open than the upland forest. This relative emptiness is apparently due to the fact that floods periodically remove both herbaceous and woody plants in the ground layer (Table 27), thus the flood plain is a naturally disturbed area. As a disturbed area, it partakes of the characteristics of a density-independent dominated habitat (Gadgil and Solbrig 1972:17, 18, 24, 26). Since the plants, including *H. helix*, are more subject to density-independent conditions, the impact of this vine (or any other species) is low. However, when the physical disturbances (floods in this case) are removed as, for example, on the upland, then density-dependent factors take over and *H. helix* would be expected to make a greater impact on the vegetation (Gadgil and Solbrig 1972:15, 16). The woody-plant data were collected after the big flood; had they been collected before, the flood-plain data might have been closer to those of the upland. To that extent, theory explains otherwise anomalous data. More data are needed for drawing more definite conclusions.

Regardless of the impact or degree of impact at the ground layer on woody vegetation by this exotic vine, there is an impact on the overstory trees and by deduction on the other layers as well. It kills them, especially the *Ulmus*. The situation appears to be as follows, and is based on the

same assumption as was made previously with the *Lonicera japonica* population: if the present percent or proportion of infestation is the same at all stages of the mature tree—alive and healthy, dying, dead standing, fallen dead—then the population is assumed to be stabilized on these trees.

Forty-two percent of the overstory *Ulmus americana* have *Hedera helix* growing on them compared to 44% which have neither this vine nor *Lonicera japonica* (Table 82). This tree species, it will be recalled, is the principal dominant on the island upland. The infestation level on dying *Ulmus* is about the same as on the healthy *Ulmus* (Table 83) and it does not differ significantly from the level on all other overstory trees (Tables 83, 84). The infestation level is virtually the same on dead and dying overstory trees except for *Ulmus*. Dead *Ulmus* has significantly more *H. helix*. What has brought this about?

Had *H. helix* been stimulated by the opening of the crowns due to dying trees as was the case with *L. japonica*, it would have been tardy in its stimulation compared with *L. japonica* (Tables 67, 68, 74, 75) and the effect would be realized after, not before, the results of *L. japonica* stimulation. In other words, the effect of such light stimulation should be reflected on the present generation of healthy trees instead of on a past generation which is reflected on dead standing trees (which in turn predates the dying generation that has a high *L. japonica* population) (Tables 83, 84).

If *Ulmus americana* wood were especially durable, like *Castanea dentata* (chestnut), then the high proportion of dead trees with the exotic vine would merely be due to an accumulation of dead trees that were tardy in falling. But *Ulmus* is not known for this kind of durability, and its relatively abundant sapwood compared to heartwood argue against this explanation (Wilson and Loomis 1967:148; Esau 1965:249, 250; Collingwood and Brush 1955:71; Koehler 1949:833, 834; Boyce 1948:448–450).

Another possibility is that *Ulmus* trees are dying off at a faster rate than they can fall. If *Ceratostomella ulmi* (Dutch elm disease fungus) were responsible, *Lonicera japonica* would almost immediately respond and the present generation of *Ulmus* would have a higher or at least as high a proportion of *L. japonica* as dying *Ulmus*. This is not the case; it is lower (Tables 82, 83), and as explained previously with the *Lonicera* discussion, the effect of *C. ulmi* has declined from a previous high.

*Hedera helix* itself appears to be killing the trees, not only *Ulmus* but other overstory and understory trees as well. The process is merely speeded up on the principal dominant. This conclusion counters the essentially dataless statement of Edlin (1970:56), who says that *H. helix* probably does not kill a tree, however, if it grows on a tree that dies, it is stimulated in two ways: (1) full light in the dead crown of the tree, and (2) increased nutrients from the soil. Edlin's main point, however, is that broad-leaved evergreens are able to utilize winter sunlight beneath



a leafless canopy of tall, broad-leaved trees and this gives such evergreens competitive power. Atanasiu (1965) found, under natural light and temperature conditions, that photosynthesis occurs in *H. helix* into late autumn up to the first days of December, then in January the plants are below the compensation point. Photosynthesis reappears in February (Atanasiu 1965). Because Theodore Roosevelt Island is closer to the equator than Europe, photosynthesis would not be expected to be as temperature-limited, so photosynthesis in *Hedera* probably occurs all winter. Since native deciduous vines can destroy native deciduous trees (Penfound 1966:187, 188), it should be expected that an evergreen vine would do the same at an accelerated rate except possibly on *Quercus* spp. and *Fagus grandifolia*; these species of Fagaceae retain their dead leaves throughout the winter and would offer some shade deterrent to an evergreen vine. As with deciduous vines, the action is apparently to shade out and break the branches of the host tree. As the tree is shaded out, growth is suppressed (Table 96) and the tree dies. This suppression would take place on *Ulmus* and other deciduous trees as well as on *Robinia pseudo-acacia* (black locust).

The sequence of events on the island which has led to the killing of overstory trees by this vine appears to be as follows. English ivy apparently was planted around the Mason mansion (see Introduction). This would have been no earlier than about 1792 (Thomas 1963:2, 11, 15; Duhamel 1935:137, 138). As the vine reached the tops of the trees or wall, it would flower in the full sunlight (Edlin 1970:55). The seeds would have been scattered by animals to account for Olmsted and Pope's report (1934:7) that the vine occurred in scattered areas as ground cover and in some of the trees. The young growth as it invades an area is not limited by light (Table 68) and, since it is a tendril liana, it does not have the disadvantage of the twiner such as *Lonicera* (see also Daubenmire 1965:305, 306). As the evergreen foliage of the vine mingles with the deciduous foliage of the tree, it begins to shade them out, growth of the tree is suppressed, and the increasingly open crown stimulates the vine already present to more luxuriant growth (Tables 68, 74) which further shades out the tree leaves.

When the trees fall either naturally or are cut, the vine increases on the trees (Table 85). The increase is significantly greater on trees other than *Ulmus* in a natural fall and significantly greater on *Ulmus* in a cut fall (Tables 85, 88). The explanation of this difference is possibly in the way the tree falls. When a tree dies, it falls apart limb by limb. Perhaps when the trunk finally falls, there are more limbs remaining on non-*Ulmus* so the opening created is larger than that for *Ulmus*, but since the *Ulmus* crown is large and spreading, it opens a larger hole in the canopy when it is cut. In either case, more light is let into the forest and this apparently stimulates *Hedera helix* growth; and if stimulated enough, it flowers and this increases the seed for further distribution.



Of course, increased light from an opened canopy does not directly stimulate new invasion (Table 68), but the old growth would be stimulated to flower (Edlin 1970:55). In addition, as more *H. helix* is present, this will be the ground cover which will not show differentiation between fallen logs and soil.

Thirteen percent of the naturally fallen *Ulmus* trees had *Hedera helix* growing on them before the fall. This is significantly greater than the 9% of all other naturally fallen trees that also had the vine before their fall (Tables 85, 88). A later generation of trees shows 38% of dying *Ulmus* and 35% of all other trees with the vine (Table 83). Although *Ulmus* has the greater percentage, this is not significant (Table 84). The present generation of healthy *Ulmus* has an even higher percentage (Table 82). The *H. helix* population, then, has increased over the years and has received direct assistance and a real boost by man when *Ulmus* is cut (Tables 85, 88).

Not only has the *H. helix* population increased, but it is taking over areas formerly occupied by *Lonicera japonica* (see Introduction and Table 96). These two factors, increased abundance and superior competition, help explain the invasion of canopy openings by new growth.

The increased abundance of *Hedera helix* on the island and on the trees is also killing the trees at a faster rate. It would kill understory trees in the same manner. American elms with *H. helix* are dying faster than other elms of the same species without *H. helix* or other trees; the dead trees are accumulating in the upright position (Table 83). The reason, apparently, is that their vigor has been lowered by the presence of Dutch elm disease. Since the fungus causing this disease experienced a high population in the recent past, an increased mortality is to be expected with *Ulmus* trees that have *Hedera* growing on them. It seems evident, that in the more remote past, *Ulmus* also experienced a period of high mortality from *H. helix*. This is indicated by the significantly higher percentage of downed *Ulmus* trees with *H. helix* before they fell naturally than all other downed trees which were infested with *Hedera* before the fall (Tables 85, 88). This former period of increased mortality on an already steadily rising rate may have been in response to the same factors as the more recent one: cutting of *Ulmus*, and the subsequent increases in populations of the smaller European engraver beetle, *Scolytus multistriatus*, and the Dutch elm disease fungus, *Ceratostomella ulmi*, which reduce tree vigor and allow *H. helix* to overpower the principal dominant at a faster rate.

English ivy is able to outcompete the herbs and trees (both stratal layers) apparently because it is evergreen and probably grows all winter in this area, while the native vegetation is dormant. It does not create its own best habitat in the sense that *Lonicera japonica* does; it apparently has relatively little influence on the nonherbaceous ground layer. By killing the trees at an accelerated rate, however, the end result of

the forest will be replacement by a *Hedera helix*-dominated community with few, if any, woody plants getting into the height of the shrub layer. This fate is similar to that described for *L. japonica*.

*Hedera helix* has been reported as a pest in its native Europe, but apparently only in disturbed habitats. Wyman (1954:46) says that in Europe it has become a pest and overruns many gardens and that it must be grubbed out in the same way we must frequently remove *L. japonica*. In succession from a conifer plantation on a drained fen in England, *H. helix* constituted 77% of the dry crop of the ground layer in an *Acer pseudoplatanus* (sycamore maple) and *Fraxinus excelsior* (European ash) woods (Kassas 1952:50, 58).

*Hedera* also dominates the ground layer in the *Fageta hederosa* (beech-English ivy) beech forests of Daghestan, Russian Soviet Federated Socialist Republic (Ljvov 1970:1246), is an important member of the ground layer in one of the *Fageto-Quercetum* (beech-oak) forest types in Báb, Czechoslovakia (Kubíček and Brechtel 1970:27, 34, 35), and in a new association *Fraxineto-Quercetum petraeae carpinuloso-hederosum*, (ash-sessile oak-horn beam-English ivy) in the Moldavian SSR, the ground cover consists of only this ivy (Geideman and Simonov 1971:84). Europe, in general, and these areas in particular are all farther north than the southeastern United States (Fernald 1950:1078) where *Hedera helix* has become naturalized. Therefore, in its natural range, temperature is probably an important factor that limits its growth and prevents it from destroying forests. If photosynthesis stops in *H. helix* for about 2 months in Romania (Atanasiu 1965), then in most of Europe it must stop for a longer period of time. In the southeastern United States, photosynthesis probably seldom stops in *Hedera*.

### *Iris pseudacorus*

Although *Iris pseudacorus* is found both close to the tidal gut and the tree line of the swamp-marsh transition, the vegetation type throughout its occurrence is dominated by *Peltandra virginica* (Table 92). The light relations are fairly uniform throughout this vegetation, with possible exceptions in June, September, and December (Tables 59-66). At these times, the transition areas may receive less light than the open marshes (Tables 60, 64, 66), but this is not clearly related to presence or absence of *I. pseudacorus*. The consistency with which the transitions receive less light than the open marsh (seven out of eight light measurement times) indicates that there may be a real, although slight, difference between the two because of the presence of the nearby trees, but more investigation would be needed to demonstrate this. Even though the *Iris* produces more biomass in the swamp-marsh transition than in the open marsh (Table 2), light is not a principal factor (Table 91). There may,

however, be a point at which light does become limiting. For example, in the shade on a wet flood plain, *Iris* seedlings were found but they never became established (Table 96).

The closest to a limiting factor that was found was the length of inundation by water as shown primarily but not entirely by topographic elevation (Tables 89–91; see also narrative Results under Replacement of Exotic *Iris*). The *I. pseudacorus* occurs in the higher areas. Although only 47% of the variation in biomass is associated with topographic elevation and hence a shorter duration of inundation by water (Table 91), it was sufficiently accurate to predict that the river level of the Potomac had risen during the growing seasons of the past several years (Table 95). The prediction was verified.

Another factor which limits *Iris pseudacorus* is *Acorus calamus* (Tables 49, 50, 96). This factor occurs only in the swamp-marsh transition. From the standpoint of water inundation, *I. pseudacorus*, in the competition experiments with *A. calamus*, was probably close to its optimum, i.e., it was not continuously inundated.

In spite of these two factors which tend to limit *I. pseudacorus* growth, this aquatic species will probably not disappear from the island by itself because of the disturbance of the habitat by man. Its impact on the aquatic ecosystem, although not quite as spectacular as that of *Hedera helix* and *Lonicera japonica* on forests, appears, nevertheless, to be considerable. This species apparently speeds up the destruction of the marsh by promoting expansion of the swamp and apparently preempts space and thus reduces the food supply of *Aix sponsa* (Linnaeus) (Wood Duck) which occurs on the island. The natural range of this duck has decreased over 30% (Martin et al. 1951:4). It has only been since 1941 that this duck generally has increased to the point that limited hunting is allowed (Martin et al. 1951:65). The sequence of events that leads to this putative impact is as follows.

Cody (1961:139, 141) says that, in Canada, the initial escape of *Iris pseudacorus* from cultivation is probably from rhizomes which have been discarded or washed by floods from low-lying gardens. Subsequent spread comes both from breaking up of the rhizomes or from the abundantly produced seed (Cody 1961:139). Possibly a similar action has taken place here. About 50 years ago, this *Iris* was, in the Washington, D.C. region, established downstream from the island (Hitchcock and Standley 1919:126). Dyke Marsh, which is located approximately 14.5 km downstream from the island, was noted by McAtee (1918:96) for the abundance of the introduced *I. pseudacorus*. It is unlikely that the *Iris* arrived on the island by either tidal action (the seeds do float) or by wild animal carrier. The seeds are rather large to be carried inadvertently on the muddy feet of birds and the species is not listed as a wildlife food (Martin et al. 1951:117, 237; Fassett 1940:347).

It is speculated that this species arrived on Theodore Roosevelt Island



the forest will be replacement by a *Hedera helix*-dominated community with few, if any, woody plants getting into the height of the shrub layer. This fate is similar to that described for *L. japonica*.

*Hedera helix* has been reported as a pest in its native Europe, but apparently only in disturbed habitats. Wyman (1954:46) says that in Europe it has become a pest and overruns many gardens and that it must be grubbed out in the same way we must frequently remove *L. japonica*. In succession from a conifer plantation on a drained fen in England, *H. helix* constituted 77% of the dry crop of the ground layer in an *Acer pseudoplatanus* (sycamore maple) and *Fraxinus excelsior* (European ash) woods (Kassas 1952:50, 58).

*Hedera* also dominates the ground layer in the *Fageta hederosa* (beech-English ivy) beech forests of Daghestan, Russian Soviet Federated Socialist Republic (Ljvov 1970:1246), is an important member of the ground layer in one of the *Fageto-Quercetum* (beech-oak) forest types in Báb, Czechoslovakia (Kubíček and Brechtel 1970:27, 34, 35), and in a new association *Fraxineto-Quercetum petraeae carpinuloso-hederosum*, (ash-sessile oak-horn beam-English ivy) in the Moldavian SSR, the ground cover consists of only this ivy (Geideman and Simonov 1971:84). Europe, in general, and these areas in particular are all farther north than the southeastern United States (Fernald 1950:1078) where *Hedera helix* has become naturalized. Therefore, in its natural range, temperature is probably an important factor that limits its growth and prevents it from destroying forests. If photosynthesis stops in *H. helix* for about 2 months in Romania (Atanasiu 1965), then in most of Europe it must stop for a longer period of time. In the southeastern United States, photosynthesis probably seldom stops in *Hedera*.

### *Iris pseudacorus*

Although *Iris pseudacorus* is found both close to the tidal gut and the tree line of the swamp-marsh transition, the vegetation type throughout its occurrence is dominated by *Peltandra virginica* (Table 92). The light relations are fairly uniform throughout this vegetation, with possible exceptions in June, September, and December (Tables 59-66). At these times, the transition areas may receive less light than the open marshes (Tables 60, 64, 66), but this is not clearly related to presence or absence of *I. pseudacorus*. The consistency with which the transitions receive less light than the open marsh (seven out of eight light measurement times) indicates that there may be a real, although slight, difference between the two because of the presence of the nearby trees, but more investigation would be needed to demonstrate this. Even though the *Iris* produces more biomass in the swamp-marsh transition than in the open marsh (Table 2), light is not a principal factor (Table 91). There may,



however, be a point at which light does become limiting. For example, in the shade on a wet flood plain, *Iris* seedlings were found but they never became established (Table 96).

The closest to a limiting factor that was found was the length of inundation by water as shown primarily but not entirely by topographic elevation (Tables 89–91; see also narrative Results under Replacement of Exotic *Iris*). The *I. pseudacorus* occurs in the higher areas. Although only 47% of the variation in biomass is associated with topographic elevation and hence a shorter duration of inundation by water (Table 91), it was sufficiently accurate to predict that the river level of the Potomac had risen during the growing seasons of the past several years (Table 95). The prediction was verified.

Another factor which limits *Iris pseudacorus* is *Acorus calamus* (Tables 49, 50, 96). This factor occurs only in the swamp-marsh transition. From the standpoint of water inundation, *I. pseudacorus*, in the competition experiments with *A. calamus*, was probably close to its optimum, i.e., it was not continuously inundated.

In spite of these two factors which tend to limit *I. pseudacorus* growth, this aquatic species will probably not disappear from the island by itself because of the disturbance of the habitat by man. Its impact on the aquatic ecosystem, although not quite as spectacular as that of *Hedera helix* and *Lonicera japonica* on forests, appears, nevertheless, to be considerable. This species apparently speeds up the destruction of the marsh by promoting expansion of the swamp and apparently preempts space and thus reduces the food supply of *Aix sponsa* (Linnaeus) (Wood Duck) which occurs on the island. The natural range of this duck has decreased over 30% (Martin et al. 1951:4). It has only been since 1941 that this duck generally has increased to the point that limited hunting is allowed (Martin et al. 1951:65). The sequence of events that leads to this putative impact is as follows.

Cody (1961:139, 141) says that, in Canada, the initial escape of *Iris pseudacorus* from cultivation is probably from rhizomes which have been discarded or washed by floods from low-lying gardens. Subsequent spread comes both from breaking up of the rhizomes or from the abundantly produced seed (Cody 1961:139). Possibly a similar action has taken place here. About 50 years ago, this *Iris* was, in the Washington, D.C. region, established downstream from the island (Hitchcock and Standley 1919:126). Dyke Marsh, which is located approximately 14.5 km downstream from the island, was noted by McAtee (1918:96) for the abundance of the introduced *I. pseudacorus*. It is unlikely that the *Iris* arrived on the island by either tidal action (the seeds do float) or by wild animal carrier. The seeds are rather large to be carried inadvertently on the muddy feet of birds and the species is not listed as a wildlife food (Martin et al. 1951:117, 237; Fassett 1940:347).

It is speculated that this species arrived on Theodore Roosevelt Island

by the deliberate dumping or planting near the tidal gut in the vicinity of an old bridge. It is around the piers of this former bridge that the greatest colony in areal extent exists. More of my plots were located here than at any other place in the open marsh. It is of note that one plot was located on top of a sheet of buried rusted metal. For *Iris pseudacorus* to survive in the wettest part of the marsh, it would have to be raised above the general level of the marsh (Table 90) so that it would not be inundated for very long (Table 91). A lowered river level along with these artificial hummocks is especially conducive to establishment (Table 95). The next largest colony is located in the vicinity of a large *Taxodium distichum* tree. Bald cypress was planted on the island in the 1930s (Thomas 1963:50). It is known that the transpiration of trees on flat lands lowers the water table (U.S. Forest Service 1954:17). Most of the other areas in the open marsh that were large enough to place plots were associated with trees either native or the introduced *T. distichum*. The critical point, then, that is going to determine whether *I. pseudacorus* or *Peltandra virginica* becomes established in the open marsh is dependent upon the presence of trash (or excessive river debris) or lowered water tables from trees. A lowered river level enhances the establishment and spread, but it should be evident that if the river level drops too far, the *Peltandra* marsh will disappear by desiccation (Results, Replacement of Exotic *Iris*). When it comes to establishment by seed, the critical point may be the millimeters difference between the larger *Peltandra* berry and the smaller *Iris* seed which apparently germinates only in moist not inundated soil.

Similar factors would operate in the establishment of *Iris pseudacorus* near the swamp tree line. Here, obviously, transpiration of trees in the growing season becomes a more important factor in lowering the water table and providing a raised support from tree roots. Here, also, because of the minor differences in topography due to the slope toward the gut (Table 89, Fig. 6), a lowered river level becomes even more important in the growth of *I. pseudacorus* (Table 91). There is another factor that enters into raising the soil level above the water level. The National Park Service has built a gravel trail through the marsh, swamp, and flood plain of the island. The erosion of the trail contributes to filling the marsh and providing habitat for the *Iris*, and the slopes of the trail side itself form an excellent habitat. Several of my swamp-marsh transition plots were located in the vicinity of this trail.

With the removal of *Peltandra virginica* habitat and its take-over by *I. pseudacorus* comes the reduction in food supply for *Aix sponsa*. Up to 25% of the diet of these ducks may come from the berries of *P. virginica* (Martin et al. 1951:447), but *I. pseudacorus* is not eaten (Martin et al. 1951:65). Stewart and Robbins (1958:21) consider this duck to be one of the primary species of breeding birds in the Coastal Plain of Maryland and the District of Columbia. In the Piedmont physiographic

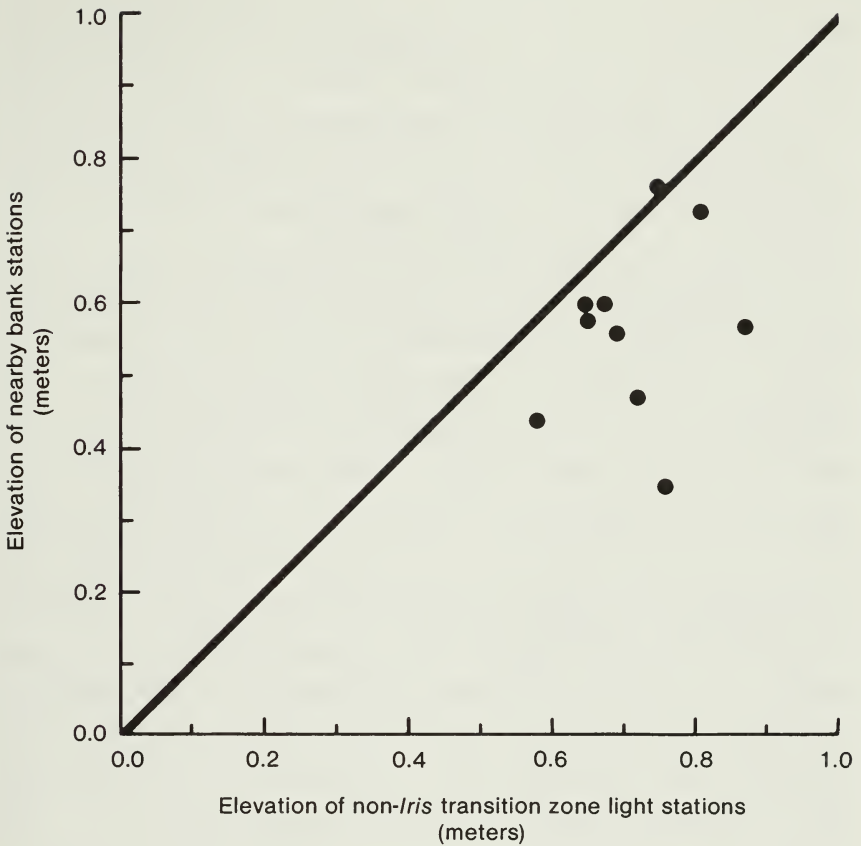


Fig. 6. Comparison of tree line stations with their bank stations in the marsh and swamp-marsh transition zone.

province, it is considered a secondary species (Stewart and Robbins 1958:29). The marsh as well as swamp and flood plain of Theodore Roosevelt Island is not only in the Coastal Plain, but is located at the very edge of the Coastal Plain (Thomas 1963:7, 39; the area marked "swamp" includes the flood plain). *Aix sponsa* males and females have been reported by me and others for this island (NPS, unpubl. data). Theoretically, then, an increase or decrease of an important food at the edge of their primary breeding range might be critical to the abundance of this duck on the island, especially during the nesting season when *Peltandra virginica* is eaten (Stewart and Robbins 1958:85; Martin et al. 1951:65).

In the swamp-marsh transition area of the marsh there is an additional impact. In the past, the swamp has been advancing on the marsh (Thomas 1963:39, 47), with the normal sequence being that the swamp trees (in

this case *Fraxinus pennsylvanica*) grow up and overtop the *Salix* (Table 96). *Salix caroliniana* (Coastal Plain willow) is closely related to *S. nigra* (Fernald 1950:504) and so is probably as intolerant of shade as *S. nigra* (Fowells 1965:652). The *Salix* (*S. nigra* black willow and *S. caroliniana*) would die out in the shaded areas of the swamp and be replaced by more shade-tolerant species. The swamp is a five-layered community (Table 76) in which the vertical structure is relatively empty, that is, few layers are represented at any given point (Table 78).

The transition area with *Iris pseudacorus* is significantly different from the area without (Tables 76, 81; narrative Results, Limiting Factors, Vegetational Strata as a Limiting Factor). The difference shown in the tables is in the woody vegetation under the overstory. The vertical structure of the *Iris* transition is more like the swamp than the non-*Iris* transition is like the swamp (Table 78). The qualitative difference between the two transitions is that the non-*Iris* area has an understory but no shrub layer and the *Iris* area is just the reverse (Table 76). Another difference is that in the non-*Iris* transition there is a dependence of the low herb layer on the understory. This correlation ceases to exist in the transition with *Iris*, and does not exist in the swamp (narrative Results, Limiting Factors, Vegetational Strata as a Limiting Factor).

The mat of *Iris* rhizomes prevents the germination and seedling development of *Salix* spp. *Salix nigra* must have exposed mineral soil for its best development (Fowells 1965:651) and with *I. pseudacorus* the soil is covered, but with *Peltandra virginica*, there is much exposed soil available. Gillham (1957:765) found, in a study of coastal vegetation, that *I. pseudacorus* was one of two chief species that occurs on non-organic soils. Rubtsoff (1959:31) found it growing along the sides of a dirt road which crosses a marsh, and my own observations show (Table 96) that it grows well on gravel. Thus, it appears that it is in very direct competition with *Salix nigra* on mineral soil. The larger *Iris* seedling apparently outgrows the *Salix* even though *S. nigra* can grow 4 ft in 1 year (Fowells 1965:651), germinates within 24 hours after falling (U. S. Forest Service 1948:328), and has a high germinative capacity (Fowells 1965:651). Apparently, *Iris* can germinate faster (Table 96) and it grows horizontally over the ground. Black willow has the disadvantage of greatly reduced viability with a few days of dry conditions (Fowells 1965:651). On the other hand, *I. pseudacorus* seed which was stored dry over winter had a germination percentage of 33 (Table 48). Although this is a low percentage, it is the same that Kartaschoff (1958:151, 152) found under favorable temperatures.

By suppressing the *Salix* spp. and providing a raised surface, the *Iris* promotes the invasion of *Fraxinus* or other trees which do not require a mineral surface. (See Fowells 1965:185-187 and U. S. Forest Service 1948:181 for *F. pennsylvanica* seedbed.) Thus, by providing a raised, moist surface rather than an inundated surface, the *I. pseudacorus* has-



tens the succession from marsh to swamp. All the transition areas which are not presently occupied by *Iris* are potential *Iris* habitat (Table 90).

*Iris* apparently increases its areal extent by creating new habitat for itself. As the rhizomes grow, they compact the soil so much that a hardpan develops (Table 94). I noticed while removing *Iris* for the biomass studies that there were often more than one layer of live rhizomes; three layers of live rhizomes were found in two of the transition plots. As the *I. pseudacorus* grows, it literally squeezes the water out of the soil to create its own drier habitat. In the areas of best *Iris* growth (the transition), this hardpan is even better developed (Table 94; tetrachoric coefficient +0.92) and results in a definite gleization of the soil (Table 93), which indicates a lack of oxygen (Lutz and Chandler 1946:408). It appears, then, that the area, the transition, where *I. pseudacorus* has the greatest impact (reduction of the *Peltandra virginica* marsh both by preempting *P. virginica* habitat and by promoting swamp invasion), is not only the area where it makes the best growth but also has the greatest potential for creating its own habitat, thus further speeding up the succession of marsh to swamp.

Raven and Thomas (1970) say that, in one place in California, *Iris pseudacorus* is growing to the complete exclusion of *Typha* and other characteristic California marsh plants and that it will spread and displace many native plants. They present no data, and perhaps some other factor such as drainage was operating. A detailed study in southern Finland (Perttula 1952) showed that *I. pseudacorus* with four other species replaced *Typha latifolia* (common cat-tail) as the first succession after a lake was drained. I found no evidence of *Typha* being replaced by *I. pseudacorus* on the island.

There are two mitigating factors which are operating to slow down the accelerated succession which is promoted by the *Iris*: *Acorus calamus* and a rising water level.

*Acorus calamus* produces rhizomes which are smaller in diameter than *I. pseudacorus*, but the mat which is formed appears to be just as rhizomatous. *Acorus* is taking over *Iris* areas in the swamp-marsh transition on the island (Table 96). *Acorus* can successfully outcompete *I. pseudacorus* under water inundation levels that appear favorable to *Iris* (Tables 49, 50), with the result that some wildlife is benefited. Araceous seeds in general are eaten by *Aix sponsa* (Fassett 1940:344, 352) although *A. calamus* produces small amounts compared to *P. virginica*. The larger benefit is with *Ondatra zibethicus* (Linnaeus), the muskrat. This resident mammal is known to feed on *A. calamus* (Fassett 1940:344). *Iris* of other species are only occasionally eaten (Fassett 1940:347; Paradiso 1969:111); the nibbled *I. pseudacorus* on the island (Table 96) possibly is in the same category. *Acorus* is not a major food of *Ondatra* (Paradiso 1969:111; Martin et al. 1951:236), but in the declining population of Maryland (Paradiso 1969:112), this araceous species may be

of some importance. The *O. zibethicus* in the marsh of Theodore Roosevelt Island are unique; they make no dome-shaped lodges, only bank dens. Paradiso (1969:112) states that the dome-shaped structure is made in the marshes, but the bank burrow is made in the banks of streams and other bodies of water.

As mentioned earlier, *Acorus calamus* produces little seed. I have never seen very many flowers of *Acorus* in the natural state and have never seen any fruits or seeds. This species puts most of its resources into vegetative structure and hence would be considered a *K*-strategist, especially when compared with *I. pseudacorus* (Table 96). *Iris pseudacorus* is an *r*-strategist. The implications are, then, that *I. pseudacorus* will be most successful in a density-independent mortality environment and *A. calamus* in a density-dependent one (see Gadgil and Solbrig 1972:14, 17–20). Both species are in the emergent zone of marsh vegetation and one might well predict on the basis of *r*- and *K*-strategy theory that as the zone fills with vegetation and density-dependent factors become more important, the *r*-strategist, *I. pseudacorus*, will not do as well, which is what is happening. About 50 years ago, *A. calamus* was common along the lower Potomac which is downstream from Washington, D.C. (Hitchcock and Standley 1919:20, 114). This species either arrived on the island after *I. pseudacorus* or if it arrived before or at the same time, it survived at a selective disadvantage or only in small areas until the habitat filled up. [The marsh is less than 200 years old (Thomas 1963:46, 47)]. The presence of *I. pseudacorus* probably did not hasten the filling process, it apparently substituted for *Peltandra virginica* as discussed earlier. This would indicate that *Acorus* would eventually take over *Peltandra* areas also since *P. virginica* is an *r*-strategist compared with *A. calamus*. The important difference, however, appears to be that with the substitution (*I. pseudacorus*), the marsh supports less wildlife, succession is short-circuited, and the marsh is shorter-lived as discussed previously.

The other mitigating factor in the growth and spread of the *Iris* is the rise in the water level of the river which has taken place for about the last decade (Table 95). As shown previously, *I. pseudacorus* decreases as length of water inundation increases (Table 91). Since the *Iris* near the tidal gut is at a lower elevation, it is affected first and has virtually disappeared (Figs. 3, 4; Tables 44, 46) and the *Peltandra* has begun to take over the *I. pseudacorus* areas (Figs. 3, 5; Tables 45, 47). The tree-line area was affected later with the same pattern of *Iris* decline and *Peltandra* increase (Figs. 2, 4, 5; Tables 42, 43, 46, 47). It is expected that *I. pseudacorus* will almost disappear in the transition area. *Peltandra* in the open marsh did not invade or respond as quickly to *Iris* decline as it did in the swamp-marsh transition. This would follow from the greater topographic differential between the exotic and nonexotic in the two marsh areas (Table 90) because it would be more difficult to float

seed to the higher elevation because the velocity of runoff is greater with higher elevations (Gilluly et al. 1955:133).

There will, however, be certain refugia, areas of higher elevation, that may be scattered around the marsh. Most of these refugia will be the result of man's activities. For example, the largest refuge is the side of the gravel trail which coincides with the tree line of the marsh-swamp transition. From these refuges, the *Iris* will spread again when the water level of the river begins to recede and the tidal inundation therefore is shortened. If the *Iris* creates new habitat for itself as suggested, then the refugia will increase in area.

### *Comparisons of the Three Exotic Species*

There is a similarity of circumstances associated with each of these three exotic species: disturbed habitats. Even in a successional stage, disturbance appears to be the key to entry. An important facet of the disturbances is that they are products of man's activity, and they have resulted in biological explosions on the island in the sense that Elton (1958:15) describes for larger areas. One of the greatest impacts of man on the environment is his introduction of exotic species into environments that he has disturbed. These introductions often trigger a sequence of events that counter the goals or best interests of man himself. Theodore Roosevelt Island is an example where the planned and unplanned activities of man, both before and since the area became a park, have set in motion biological forces which are destined, unless countered, to destroy the upland and flood-plain forests and the marshes.

It is to be expected that different organisms might have different degrees of impact on a given environment. The same organism in closely related environments may have widely differing impacts. On the basis of resources taken out of circulation in the form of dry biomass, the three exotic species in the six microhabitats present four grades of impact, with *Iris pseudacorus* in the transition having the greatest and *Lonicera japonica* in a mildly disturbed forest (natural understory), the least (Table 2). The fact that an herb has a greater control of the environment than a woody plant should not be too surprising since the herb in question, *I. pseudacorus*, is in the tall herb layer of its vegetation type which has only four layers (Table 76), while the woody vines, as studied, are in a subordinate layer in their type which has five layers.

*Hedera helix* and *L. japonica* live in similar habitats. The mildly disturbed forest with *L. japonica* is identical with the upland *H. helix* forest in the light intensity that reaches the forest floor (Tables 51-58). In vertical structure, they are the same in number of layers (Tables 76, 77), in the relative emptiness of the layers (Table 78), and in the relative variability of the depth of the woody layers (Table 81). There is, however,



one aspect of vertical structure where they differ. Forests with *H. helix* have a significant correlation of one of the woody layers with another woody layer, whereas this is not the case with *L. japonica* (Table 80). Since, in the case of the upland *H. helix* forest, the correlation is between overstory and understory trees, and since it is only rather recently that *H. helix* has been extremely abundant, this correlation is probably not the result of *H. helix* impact, but probably a condition conducive to *Hedera* invasion. *Lonicera* which has been abundant on the island for a long time (Thomas 1963:49), was apparently more abundant than *H. helix* until recently (Introduction), and has generally a greater suppression of trees especially in much disturbed habitats, is possibly the creator of the correlations that are found both in the upland and flood-plain *Hedera* forests.

The fall of any canopy tree in the forest, from any cause, increases the abundance of both exotic vines, but not equally (Table 85). Natural falls of trees other than *Ulmus americana* promote *Hedera helix* more than a natural fall of *Ulmus*, but *Ulmus* which is cut down stimulates growth of *Hedera* more than other trees which are cut.

The increased presence of these two exotic vines with fallen trees appears to be due mostly to the increase in light. Both species respond to an increase in light or a decrease in shade (Tables 67, 68, 74, 75), but they do not respond equally. *Lonicera* is more dependent upon light than *H. helix*, and in *Lonicera* this dependence is greater with new growth than old growth (Table 67), but the reverse is true of *Hedera* (Table 68). In *Hedera*, chlorophyll A formation takes place at a faster rate than leaf biomass (Table 74). Climax dominants in layered vegetation must be shade-tolerant while young (Daubenmire 1965:229, 230; Oosting 1956:92). *H. helix* appears to behave like a climax dominant.

*Hedera* not only has a greater biomass per square meter than *Lonicera japonica* regardless of habitat (Table 2), but in mildly disturbed upland forests, it grows faster per unit of time (Tables 5, 6, 7, 96). The impact of the biomass, however, differs between the vines and the life forms that they suppress. For example, in mildly disturbed forests, *H. helix* suppresses herbs more than *L. japonica* does (Table 38), and the tendency is for *L. japonica* to suppress trees more than *H. helix* under the same disturbance conditions (Table 40). Under severe disturbance conditions, *L. japonica* definitely suppresses trees in the ground layer more than any *H. helix* on the island. Woody plants other than trees are suppressed about equally by the exotic vines (Table 41). Biologically, the two exotic vines combined suppress the reproduction of *Podophyllum peltatum* (Table 32), but the increase after release was not great enough to be statistically significant. This is probably due to the low number of replications available.

With *Lonicera japonica* suppressing woody plants, particularly trees, and growing over shrubs and small trees and killing them, and *Hedera*



*helix* killing the larger trees and suppressing herbs, the upland and flood-plain forests are slowly disappearing and will be replaced by a vine-dominated community. *Hedera* has taken over *L. japonica* areas (Table 96 and Introduction) and is able to accumulate biomass faster than *Lon-icera*. The final community will be dominated by *Hedera helix*. The only forests on the island will be those of the swamp which will have increased in size due to the destruction of the marsh by *Iris pseudacorus*.



Habitat of *Lonicera japonica* (Japanese honeysuckle) in a natural understory. Vine climbing a small tree.

## Conclusions

The introduction, establishment, and spread of all three exotic species is associated with a habitat disturbed by man, and each of these species is in turn bringing about major changes in the island ecosystem.

Replicated experiments verified the surveys which show that light is a strong limiting factor for *Lonicera japonica*. Depending upon circumstances, both herbs and woody plant reproduction are suppressed. However, even in the mildly disturbed forest, tree reproduction is suppressed. *Ulmus americana*, *Prunus serotina*, *Liriodendron tulipifera*, which are among the important dominant trees of the island, are more sensitive to *Lonicera japonica* presence than other trees. *Lonicera*, once it is established, creates its own sunny habitat by changing the vertical structure of the forest both through suppression of reproduction and strangling and shading out vegetation up to the size of small trees. The cutting down of trees further promotes this exotic vine as does the fungus *Ceratostomella ulmi* when it produces dying *Ulmus americana* trees.

Replicated experiments and surveys also show that on the island upland no single factor is more important than light for mature *Hedera helix* growth. *Hedera*, however, does not respond as quickly in growth to increased light as *L. japonica* does. This may be because *H. helix* is more of a climax species, which in turn may be related to its forming chlorophyll A slightly faster than leaf biomass as a whole. A high water table appears to be a limiting factor for *Hedera* on the flood plain. Regardless of habitat, *H. helix* prevents the reproduction of herbs, especially on the island upland. On the flood plain, the destruction of herbs by this exotic vine is about the same as that of a hurricane-force flood. The vine also kills trees in the overstory and understory by shading them out. Although the opening left by falling overstory trees increases the growth of *H. helix*, a significantly greater increase is brought about by cutting elm (*Ulmus americana*) trees rather than by cutting other canopy trees.

Apparently, *Lonicera japonica* has produced a peculiar structural change (high correlation of one vegetational layer with another) that is conducive to invasion by *Hedera helix*, and between the two of these vines, all the forests on the island, except the swamp, are being killed.

*Hedera* is outcompeting *Lonicera*, and it is projected that it will dominate the vine community.

It is in error to suppose that light relations are preserved in a forest as long as the canopy trees remain. The removal of vegetation in the lower layers disturbs the light relations sufficiently to encourage these exotic vines.

The factor that most nearly approaches a limiting factor for *Iris pseudacorus* in the marshes of the island is the time length of water inundation. The longer the inundation, the more poorly it does. A second important factor is the presence of *Acorus calamus* in the swamp-marsh transition. This species is able to take over *Iris* areas near the tree line. When the water level drops during the growing season and trash is deposited in the marsh, conditions are favorable to *I. pseudacorus* which begins replacing *Peltandra virginica*, an important food for the Wood Duck. As the *Iris* grows, it apparently creates habitat favorable to itself and in the swamp-marsh transition its presence speeds up succession from marsh to swamp in an abnormal manner, with the end result being little or no marsh. The present rising water level in the river during the growing season is slowing the succession down, but it will not entirely eliminate the *Iris*.



# Tables

TABLE 1. Comparison of combined control plot frequency (from square decimeter grid) by pooled chi-square except as noted<sup>a</sup>

Species and Habitat	1971 Observation	1972 Observation	Significance
Upland <i>Hedera</i>	1000	1000	no change
Flood-plain <i>Hedera</i>	799	800	not significant at 0.1
Natural understory <i>Lonicera</i>	785	785	no change
Cleared understory <i>Lonicera</i>	1000	1000	no change
Transition <i>Iris</i>	1211	1240	significant at 0.005
Open marsh <i>Iris</i>	684	569	<sup>a</sup> 5 individual $\chi^2$ out of 7 significant beyond 0.001; 2 $\chi^2$ not significant

TABLE 2. Comparison of dry-weight biomass dominance in g/m<sup>2</sup> of three exotic species in two habitats each from a simple random sampling design survey

Characteristics	Species and Habitats					
	<i>L. japonica</i> natural understory	<i>L. japonica</i> cleared understory	<i>I. pseudacorus</i> open marsh	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>I. pseudacorus</i> transition
Observation dates	4/9-10/71	4/13-15/71	6/10-18/71	4/22-29/71	4/16-22/71	5/3-15/71
No. m <sup>2</sup> plots	11	10	15	20	20	20
Standard deviation	40 g	50 g	238 g	106 g	84 g	310 g
Mean g/m <sup>2</sup>	113 g	298 g	371 g	407 g	425 g	1105 g
Duncan's 5% test	_____					
Note: any two means underscored by the same line are not significantly different; any two means not underscored by the same line are significantly different.						

Analysis of variance:  $F_{3/90} \text{ at } = 59.462$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{15} \text{ at } = 76.113$ ; significant variance beyond 0.001.

Biology: Upland and flood-plain *Hedera* each appear to be different from cleared understory *Lonicera*. Modified and unmodified *t* tests show significance beyond 0.001 for the first comparison and a modified *t* test for the second shows significance at 0.005.

TABLE 3. Comparison of dm<sup>2</sup> grid frequency dominance in f/m<sup>2</sup> of three exotic species in two habitats each from a simple random sampling design survey

Characteristics	Species and Habitats					
	<i>I. pseudacorus</i> transition	<i>I. pseudacorus</i> open marsh	<i>L. japonica</i> natural understory	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> cleared understory
Observation dates	4/2-5/71	4/2-5/71	3/31-4/1/71	4/1-5 and 22, 23/71	3/31/71	4/12, 13/71
No. m <sup>2</sup> plots	33	22	19	28	30	20
Original F. Data						
Standard deviation	5.1	4.2	3.7	0.2	0	0
Mean f/m <sup>2</sup>	92.8	96.1	98.4	100.0	100.0	100.0
Duncan's 5% test	—	—	—	—	—	—
Arc Sine Trans. Data						
Mean f/m <sup>2</sup>	75.5	80.6	86.5	89.8	90.0	90.0
Duncan's 5% test	—	—	—	—	—	—
Corrected mean	93.8	97.4	99.6	100.0	100.0	100.0

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance: Original data,  $F_{3/146} \text{ at } = 25.177$ ; significant beyond 0.001; transformed data,  $F_{3/146} \text{ at } = 52.665$ ; significant beyond 0.001. Bartlett's:  $\chi^2_{3 \text{ at }} = 655.432$  (f) and 613.186 (transformed); significant variance beyond 0.001. Biology: As shown by original frequency data.

TABLE 4. Comparison of cover dominance in  $\text{dm}^2/\text{m}^2$  of *Hedera helix* in two habitats from a simple random sampling design survey

Characteristics	Habitats	
	Upland	Flood plain
Observation dates	3/31/71	4/1-5/71 and 22, 23/71
No. $\text{m}^2$ plots	30	28
Standard deviation	1.0	2.7
Mean $\text{dm}^2/\text{m}^2$	99.7	98.7

Modified  $t$  test

$t' = 1.904$ ; significant at 0.1 (Snedecor);

$t_{34 \text{ df}} = 1.904$ ; significant at 0.1 (Satterthwaite).

Variance ratio:  $F_{27/29 \text{ df}} = 6.906$ ; significant variance beyond 0.001.



TABLE 5. Comparison of growth over time of dry-weight biomass, g/m<sup>2</sup>, for two species, each in two habitats

Experiments	Results			
	Experimental design	m <sup>2</sup> plot replications	Standard deviation	Mean g/m <sup>2</sup>
Upland <i>Hedera</i> , 1 year	paired plot	10	39.6	87.1
1.25 years		10	64.0	108.2
Flood-plain <i>Hedera</i> 1 year	complete randomization	7	20.0	36.0
1.25 years		8	12.0	10.6
Natural understory <i>Lonicera</i> 1 year	complete randomization	3	13.1	16.7
1.25 years		8	21.4	30.2
Cleared understory <i>Lonicera</i> 1 year	paired plot	10	58.5	216.7
90 days		10	26.9	85.9

$t_{9 \text{ df}} = 1.521$   
 modified  $t_{9 \text{ df}} = 0.886$ ; not significant at 0.1  
 $t_{13 \text{ df}} = 3.025$ ; significant at 0.01  
 $t_{9 \text{ df}} = 1.011$ ; not significant at 0.1  
 modified  $t_{9 \text{ df}} = 6.424$ ; significant beyond 0.001

TABLE 6. Comparison of 1 year dry-weight biomass growth ( $\text{g/m}^2$ ) in two habitats each for *H. helix* and *L. japonica* from a completely randomized design experiment

Characteristics	Species and Habitats			
	<i>L. japonica</i> natural understory	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> cleared understory
No. $\text{m}^2$ plots	3	7	10	10
Standard deviation	13.1	20.0	39.6	58.5
Mean $\text{g/m}^2$	16.7	36.0	87.1	216.7
Duncan's 5% test				

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/26 \text{ df}} = 33.368$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{3 \text{ df}} = 10.504$ ; significant at 0.02.

Biology: The means underscored in Duncan's test also appear to be significantly different from each other. An unmodified *t* test shows no significance at 0.1 between natural understory *Lonicera* and flood-plain *Hedera*.

TABLE 7. Comparison of 1.25 years of dry-weight biomass growth ( $\text{g/m}^2$ ) in two habitats of *H. helix* and one habitat of *L. japonica* from a completely randomized design experiment

Characteristics	Species and Habitats		
	<i>H. helix</i> flood plain	<i>L. japonica</i> natural understory	<i>H. helix</i> upland
No. $\text{m}^2$ plots	8	8	10
Standard deviation	12.0	21.4	64.0
Mean $\text{g/m}^2$	10.6	30.2	108.2
Duncan's 5% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{2/23 \text{ df}} = 13.695$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{2 \text{ df}} = 19.739$ ; significant beyond 0.001.

Biology: The two means underscored in Duncan's test appear as though they should be significantly different. Unmodified and modified *t* tests show they are significantly different at the 0.05 level.

TABLE 8. Comparison of growth over time by frequency ( $f/m^2$ ) from  $dm^2$  grid in upland *H. helix* from a randomized block design experiment replicated 10 times (and a paired plot design experiment)

Characteristics	Treatments		
	1 year of growth	1.25 years of growth	control no treatment
Original F. Data			
Standard deviation	14.8	6.6	0.0
Mean $f/m^2$	86.6	94.8	100.0
Arc Sine Trans. Data			
Mean $f/m^2$	71.1	80.5	90.0
Corrected mean	89.5	97.3	100.0

Bartlett's:  $\chi^2_{2 \text{ df}}$  original data = 100.333; significant variance beyond 0.001; arc sine transformed = 95.066; significant variance beyond 0.001;  $\sqrt{(100 - x) + 0.5}$  trans. = 61.264; significant variance beyond 0.001; logarithmic trans. = 12.292; significant variance at 0.005.

Paired plot design experiment: One year and 1.25 years of growth;

Results: Original data, modified  $t_{9 \text{ df}} = 1.600$ ; not significant at 0.1; arc sine transformed data,  $t_{9 \text{ df}} = 6.489$ ; significant beyond 0.001.

Biology: There are probably no real differences between the control and 1.25 years of growth, but the data seem to indicate differences with the two other comparisons.

TABLE 9. Comparison of growth over time by frequency ( $f/m^2$ ) from  $dm^2$  grid in natural understory *L. japonica* from a randomized block design experiment with three replications

Characteristics	Treatments		
	1.25 years of growth	1 year of growth	control no treatment
Original F. Data			
Standard deviation	31.5	34.1	6.9
Mean $f/m^2$	58.3	60.3	96.0
Duncan's 10% test			
5% test			
Arc Sine Trans. Data			
Mean $f/m^2$	50.7	51.4	83.2
Duncan's 1% test			
Corrected mean	59.9	61.1	98.6

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance: Original data,  $F_{2/4 \text{ df}} = 5.092$ ; significant at 0.1; transformed data,  $F_{2/4 \text{ df}} = 20.623$ ; significant at 0.01.

Bartlett's:  $\chi^2_{2 \text{ df}} = 3.937$  (original) and 0.716 (transformed); no significant variance at 0.1.

TABLE 10. Comparison of growth over time by frequency ( $f/m^2$ ) from  $dm^2$  grid in natural understory *L. japonica* from a completely randomized design experiment (includes data from the randomized block experiment summarized in Table 9)

Characteristics	Treatments		
	1 year of growth	1.25 years of growth	control no treatment
No. $m^2$ plots	3	8	8
Original F. Data			
Standard deviation	34.1	25.7	4.2
Mean $f/m^2$	60.3	79.2	98.4
Duncan's 5% test			
Arc Sine Trans. Data			
Mean $f/m^2$	51.4	67.7	86.5
Duncan's 5% test			
Corrected means	61.1	85.6	99.6

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance: Original data,  $F_{2/16 \text{ df}} = 3.977$ ; significant at 0.05; transformed data,  $F_{2/16 \text{ df}} = 5.964$ ; significant at 0.025.

Bartlett's:  $\chi^2_{2 \text{ df}} = 17.804$ ; significant variance beyond 0.001 (original) and 7.226; significant variance at 0.05 (transformed).

Biology: No real differences.

TABLE 11. Comparison of 1 year of growth with control by frequency ( $f/m^2$ ) from  $dm^2$  grid in flood-plain *H. helix* from a paired plot design experiment with seven replications

Characteristics	Treatments (April readings)	
	control	1 year of growth
Original F. Data		
Standard deviation	0	28.1
Mean $f/m^2$	100	64.1
Arc Sine Trans. Data		
Mean $f/m^2$	90	54.0
Corrected mean	100	65.5

Modified  $t$  tests:  $t_{6 \text{ df}} = 3.379$ ; significant at 0.02 for original data; and  $t_{6 \text{ df}} = 5.354$ ; significant at 0.005 for transformed data.

Variance ratio:  $F_{\text{orig.}} = 787809.52$  and  $F_{\text{trans.}} = 315647.33$ ; both are significant beyond 0.001.

Individual  $\chi^2_{1 \text{ df}}$  for each pair of plots: five out of seven pairs show significant differences (one pair at 0.05, one pair at 0.01, one pair at 0.005, and two pairs beyond 0.001).

Heterogeneity  $\chi^2_{6 \text{ df}} = 47.268$ ; significant beyond 0.001.



TABLE 12. Comparison of 1.25 years of growth with control (after the flood of Hurricane Agnes) by frequency (f/m<sup>2</sup>) from dm<sup>2</sup> grid in flood-plain *H. helix* from a paired plot design experiment with eight replications

Characteristics	Treatments (July readings)	
	control	1.25 years of growth
Original F. Data		
Standard deviation	37.3	24.6
Mean f/m <sup>2</sup>	64.2	30.1
Arc Sine Trans. Data		
Mean f/m <sup>2</sup>	57.3	30.8
Corrected mean	70.9	26.1

$t$  tests:  $t_{7 \text{ df}} = 5.058$  (original) and 4.879 (transformed); both significant at 0.005.

Variance ratio:  $F_{\text{orig.}} = 2.293$  and  $F_{\text{trans.}} = 2.727$ ; both are not significant at 0.1.

Individual  $\chi^2_{1 \text{ df}}$  for each pair of plots: all eight pairs show significant differences (one pair at 0.05, one pair at 0.005, and six pairs beyond 0.001).

Heterogeneity  $\chi^2_{7 \text{ df}} = 2031.657$ ; significant beyond 0.001.

TABLE 13. Comparison of 1 year with 1.25 years of growth by frequency (f/m<sup>2</sup>) from dm<sup>2</sup> grid in flood-plain *H. helix* from a paired plot design experiment with seven replications

Characteristics	Treatments	
	1 year of growth	1.25 years of growth
Original F. Data		
Standard deviation	28.1	20.8
Mean f/m <sup>2</sup>	64.1	24.7
Arc Sine Trans. Data		
Mean f/m <sup>2</sup>	54.0	27.2
Corrected mean	65.5	20.9

$t$  tests for paired plots:  $t_{6 \text{ df}} = 2.987$  (original) and 2.877 (transformed); significant at 0.025 and 0.05, respectively.

Variance ratio:  $F_{\text{orig.}} = 1.818$  and  $F_{\text{trans.}} = 1.210$ ; both are not significant at 0.1

Individual  $\chi^2_{1 \text{ df}}$  for each pair of plots: all seven pairs show significant differences (one pair at 0.02 and six pairs beyond 0.001).

Heterogeneity  $\chi^2_{6 \text{ df}} = 1053.588$ ; significant beyond 0.001.

TABLE 14. Comparison of 1 year of growth with control by frequency ( $f/m^2$ ) from  $dm^2$  grid in cleared understory *L. japonica* from a paired plot design experiment with 10 replications

Characteristics	Treatments	
	control no treatment	1 year of growth
Original F. Data		
Standard deviation	0	0.7
Mean $f/m^2$	100	99.7
Arc Sine Trans. Data		
Mean $f/m^2$	90	88.6
Corrected mean	100	99.9

Modified  $t$  tests:  $t_{9 \text{ df}} = 1.405$  (original) and 1.472 (transformed); both are not significant at 0.1

Variance ratio:  $F_{\text{orig.}} = 455.55$  and  $F_{\text{trans.}} = 8866.77$ ; both are significant beyond 0.001.

Pooled  $\chi^2_{1 \text{ df}} = 0.009$ ; not significant at 0.1.

Heterogeneity  $\chi^2_{9 \text{ df}} = 0.041$ ; not significant at 0.1.

TABLE 15. Comparison of 90 days of growth with control by frequency ( $f/m^2$ ) from  $dm^2$  grid in cleared understory *L. japonica* from a paired plot design experiment with 10 replications

Characteristics	Treatments	
	control no treatment	90 days of growth
Original F. Data		
Standard deviation	0.0	0.3
Mean $f/m^2$	100.0	99.9
Arc Sine Trans. Data		
Mean $f/m^2$	90.0	89.4
Corrected mean	100.0	100.0

Modified  $t$  tests:  $t_{9 \text{ df}} = 1.000$  (original) and 1.000 (transformed); both are not significant at 0.1.

Variance ratio:  $F_{\text{orig.}} = 100.00$  and  $F_{\text{trans.}} = 3293.80$ ; both are significant beyond 0.001.

Pooled  $\chi^2_{1 \text{ df}} = 0.001$ ; not significant at 0.1

Heterogeneity  $\chi^2_{9 \text{ df}} = 0.009$ ; not significant at 0.1.

TABLE 16. Comparison of 1 year with 90 days (0.25 year) of growth by frequency ( $f/m^2$ ) from  $dm^2$  grid in cleared understory *L. japonica* from a paired plot design experiment with 10 replications

Characteristics	Treatments	
	90 days of growth	1 year of growth
Original F. Data		
Standard deviation	0.3	0.7
Mean $f/m^2$	99.9	99.7
Arc Sine Trans. Data		
Mean $f/m^2$	89.4	88.6
Corrected mean	100.0	99.9

Modified  $t$  tests:  $t_{9 \text{ df}} = 0.848$  (original) and  $0.737$  (transformed); both are not significant at 0.1.

Unmodified  $t$  test for transformed data:  $t_{9 \text{ df}} = 1.0$ ; not significant at 0.1.

Variance ratio:  $F_{\text{orig.}} = 4.555$ , significant at 0.025;  $F_{\text{trans.}} = 2.691$ , significant at 0.1.

Individual  $\chi^2_{1 \text{ df}}$  for each pair of plots: all 10 pairs not significant at 0.1.

Heterogeneity  $\chi^2_{9 \text{ df}} = -3.964$ ; significant (note negative number).

TABLE 17. Comparison of 1 year of growth by frequency ( $f/m^2$ ) from  $dm^2$  grid in two habitats each for *L. japonica* and *H. helix* by a complete randomization design experiment

Characteristics	Species and Habitats			
	<i>L. japonica</i> natural understory	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> cleared understory
No. $m^2$ plots	3	7	10	10
Original F. Data				
Standard deviation	34.1	28.1	14.8	0.7
Mean $f/m^2$	60.3	64.1	86.6	99.7
Duncan's 5% test				
Arc Sine Trans. Data				
Mean $f/m^2$	51.4	54.0	71.1	88.6
Duncan's 5% test				
Corrected mean	61.1	65.5	89.5	99.9

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance, original data:  $F_{3/26 \text{ df}} = 6.673$ ; significant at 0.005; transformed data:  $F_{3/26 \text{ df}} = 12.901$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{3 \text{ df}} = 56.557$  (original) and  $20.772$  (transformed); both are significant beyond 0.001.

Biology: Appears as Duncan's test shows.

TABLE 18. Comparison of 1.25 years of growth by frequency ( $f/m^2$ ) from  $dm^2$  grid in natural understory *L. japonica* and two habitats each of *H. helix* by a complete randomization design experiment

Characteristics	Species and Habitats		
	<i>H. helix</i> flood plain	<i>L. japonica</i> natural understory	<i>H. helix</i> upland
No. $m^2$ plots	8	8	10
Original F. Data			
Standard deviation	24.6	25.7	6.6
Mean $f/m^2$	30.1	79.2	94.8
Duncan's 5% test	—	—	—
Arc Sine Trans. Data			
Mean $f/m^2$	30.8	67.7	80.5
Duncan's 10% test	—	—	—
Corrected mean	26.2	85.6	97.3

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance, original data:  $F_{2/23 \text{ df}} = 24.316$ ; significant beyond 0.001; transformed data:  $F_{2/23 \text{ df}} = 21.765$ ; significant beyond 0.001.

Bartlett's  $\chi^2_{2 \text{ df}} = 13.553$  (original), significant at 0.005; and 4.238 (transformed), not significant at 0.1.

Biology: As shown by Duncan's test (modified analysis of variance on original data).

TABLE 19. Comparison of growth over time by area covered ( $dm^2/m^2$ ) in upland *H. helix* from a randomized block design experiment replicated 10 times (and three paired plot experiments)

Characteristics	Treatments		
	1 year of growth	1.25 years of growth	control no treatment
Standard deviation	25.8	18.6	0.2
Mean $dm^2/m^2$	70.2	82.4	99.9

Bartlett's:  $\chi^2_{2 \text{ df}}$  original data = 71.505; significant variance beyond 0.001; arc sine transformed = 29.391; significant variance beyond 0.001;  $\sqrt{(100 - x) + 0.5}$  trans. = 40.980; significant variance beyond 0.001; logarithmic trans. = 81.175; significant variance beyond 0.001.

Biology: There appears to be significant differences among all the means.

Paired plot analysis of randomized block data;

results: control and 1 year growth, modified  $t_{9 \text{ df}} = 3.639$ ; significant at 0.01;  
control and 1.25 years growth, modified  $t_{9 \text{ df}} = 2.959$ ; significant at 0.02;  
1 year and 1.25 years growth, unmodified  $t_{9 \text{ df}} = 4.285$ ; significant at 0.005.



TABLE 20. Comparison of growth over time by area covered ( $\text{dm}^2/\text{m}^2$ ) in flood-plain *H. helix* from a series of paired plot experiments

Experiments	Results			Significance
	$\text{m}^2$ plot replications	Standard deviation	Mean $\text{dm}^2/\text{m}^2$	
Control and one year of growth	7	3.6	97.6	modified $t_6$ at = 8.795; significant beyond 0.001
	7	19.5	31.7	
Control and 1.25 years of growth	8	28.9	40.1	modified $t_7$ at = 2.203; significant at 0.1
	8	12.9	15.4	
One year of growth and 1.25 years of growth	7	19.5	31.7	$t_6$ at = 2.509; modified $t_9$ at = 2.304; both significant at 0.05
	7	10.5	12.4	

TABLE 21. Comparison of 1 year of cover growth ( $\text{dm}^2/\text{m}^2$ ) in two habitats of *H. helix* from a completely randomized design experiment

Characteristics	Habitats	
	upland	flood plain
No. $\text{m}^2$ plots	10	7
Standard deviation	25.8	19.5
Mean $\text{dm}^2/\text{m}^2$	70.2	31.7

$t$  test:  $t_{15 \text{ df}} = 3.324$ ; significant at 0.005.

Variance ratio:  $F_{9/6 \text{ df}} = 1.749$ ; not significant at 0.1.

TABLE 22. Comparison of 1.25 years of cover growth ( $\text{dm}^2/\text{m}^2$ ) in two habitats of *H. helix* from a completely randomized design experiment

Characteristics	Habitats	
	upland	flood plain
No. $\text{m}^2$ plots	10	8
Standard deviation	18.6	12.9
Mean $\text{dm}^2/\text{m}^2$	82.4	15.4

$t$  test:  $t_{16 \text{ df}} = 8.631$ ; significant beyond 0.001.

Variance ratio:  $F_{9/7 \text{ df}} = 2.082$ ; not significant at 0.1.

TABLE 23. Description of flood and its effects as a result of Hurricane Agnes from two surveys

Surveys	Results			
	Survey design	Observation replications	Mean	Confidence limits and probability level
Flood crest height <sup>a</sup> in meters, 24 June 1972	not random	5	4.34	3.62-5.05 at 0.1
Mud depth in CENTIMETERS, 25-28 July 1972	simple random sampling	31	7.8	5.9-9.7 at 0.01
				0.0-13.0

<sup>a</sup> Datum is mean sea level.

TABLE 24. Influence of *H. helix* and other ground cover on mud deposition in cm from Hurricane Agnes flood from a randomized block experiment replicated seven times; observations made 25–28 July 1972

Characteristics	Treatments		
	ground cover removed April 1972	control, no ground cover removed	ground cover removed April 1971
Standard deviation	3.7	2.8	2.5
Mean cm	8.1	8.3	9.4
Duncan's 10% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{2/12 \text{ df}} = 1.748$ ; not significant at 0.1.

Bartlett's:  $\chi^2_{2 \text{ df}} = 0.984$ ; not significant at 0.1.

TABLE 25. Flood survival of *H. helix* on the flood plain in frequency per m<sup>2</sup> from dm<sup>2</sup> grid by a paired (in time) plot (1 × 1 m) design survey replicated seven times

Characteristics	Observations	
	25-28 July 1972	26-29 April 1972
Total F., all plots	414	700
Mean f/m <sup>2</sup>	59.1	100.0

Individual  $\chi^2_{1 \text{ df}}$  for each pair of plots: five out of seven pairs show significant differences (one pair at 0.1, and four pairs beyond 0.001).

Heterogeneity  $\chi^2_{6 \text{ df}} = 82.608$ ; significant beyond 0.001.

TABLE 26. Flood survival of *H. helix* on the flood plain in dm<sup>2</sup> of cover per m<sup>2</sup> by a paired (in time) plot (1 × 1 m) survey design replicated seven times

Characteristics	Observations	
	25-28 July 1972	26-29 April 1972
Standard deviation	24.4	3.6
Mean dm <sup>2</sup> /m <sup>2</sup>	33.7	97.6

Paired plot design: Modified  $t_{6 \text{ df}} = 6.865$ ; significant beyond 0.001.

Variance ratio:  $F = 46.687$ ; significant beyond 0.001.



TABLE 27. Flood survival of woody plants, herbaceous plants, and comparisons of woody and herbaceous plants on the flood plain by numbers from paired (in time) m<sup>2</sup> plots from several surveys; all data were square root ( $\sqrt{x + 0.5}$ ) transformed before analysis

Surveys	Results				Significance
	No. of m <sup>2</sup> plots	Standard deviation	Mean no./m <sup>2</sup>	Corrected mean no./m <sup>2</sup>	
Woody species					
26-29 April 1972	7	7.7	8.1	6.6	modified $t_6$ at = 2.528; significant at 0.05
25-28 July 1972	7	1.6	1.4	1.1	
<i>Acer negundo</i>					
26-29 April 1972	7	6.8	4.6	3.1	modified $t_6$ at = 2.377; significant at 0.1
25-28 July 1972	7	0.0	0.0	0.0	
<i>Lindera benzoin</i>					
26-29 April 1972	7	1.5	1.0	0.7	$t_6$ at = 2.067; significant at 0.1
25-28 July 1972	7	0.8	0.4	0.3	
Herbaceous species					
18 May 1972	7	6.5	6.0	4.4	$t_6$ at = 3.098; significant at 0.025
25-28 July 1972	7	2.6	1.3	0.8	modified $t_6$ at = 1.793; not significant at 0.1
Herbs vs. woody	7 pairs	—	—	—	$t_6$ at = 0.488; not significant at 0.1

TABLE 28. Comparison of herbaceous and woody plants in upland *H. helix* weeded (treated) and unweeded (control)  $1 \times 1$  m plots by paired plot design experiments on square root ( $\sqrt{x + 0.5}$ ) transformed data (no./m<sup>2</sup>)

Experiments	m <sup>2</sup> plot replications	Results						Corrected mean 1971	Corrected mean 1972	Significance
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972					
Herbs controls treated	10	25.0	47.5	11.8	24.2		4.1	10.1	modified $t_9$ at = 8.306; significant beyond 0.001	
	10	21.5	57.1	8.5	101.8		2.9	93.4		
Woody controls treated	10	1.0	4.3	0.4	3.3		0.3	2.3	$t_9$ at = 2.244; significant at 0.1	
	10	1.3	3.3	0.5	5.9		0.3	5.3		
Herbs vs. woody	10	—	—	—	—		—	—	modified $t_9$ at = 6.501; significant beyond 0.001	
	10	—	—	—	—		—	—		
Trees controls treated	10	0.3	1.0	0.1	0.4		0.1	0.3	modified $t_9$ at = 1.700; not significant at 0.1	
	10	0.0	1.8	0.0	1.1		0.0	0.8		
Other woody controls treated	10	0.9	3.6	0.3	2.9		0.2	2.0	$t_9$ at = 1.843; significant at 0.1	
	10	0.7	3.0	0.3	4.6		0.2	4.1		

TABLE 29. Comparison of herbs, trees, and other woody plants in upland *H. helix* habitat by a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control (*H. helix* unweeded) and treated (*H. helix* weeded) plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Life Form		
	Trees	Other woody	Herbs
No. m <sup>2</sup> plots	10	10	10
Trans. mean differences	0.3	0.5	6.7
Duncan's 5% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{2/27 \text{ df}} = 45.634$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{2 \text{ df}} = 20.491$ ; significant variance beyond 0.001.

Biology: Probably as indicated by Duncan's test.

TABLE 30. Comparison of herbaceous and woody plants in natural understory *L. japonica* weeded (treated) and unweeded (control) 1 × 1-m plots by paired plot design experiments (except herbs vs. woody which was a completely randomized design) on square root ( $\sqrt{x + 0.5}$ ) transformed data (no./m<sup>2</sup>)

Experiments	m <sup>2</sup> plot replications	Results						Significance
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972	Corrected mean 1971	Corrected mean 1972	
Herbs								
controls	3	0.6	5.5	0.3	6.3	0.3	5.0	$t_2$ at = 1.923; modified
treated	3	12.1	31.2	9.3	39.0	6.4	35.0	$t_2$ at = 2.402; not significant at 0.1
Woody								
controls	8	0.8	20.7	0.5	11.4	0.4	7.0	$t_7$ at = 2.392; significant
treated	8	0.5	14.0	0.4	23.6	0.3	21.7	at 0.05
Herbs vs. woody	3	—	—	—	—	—	—	$t_9$ at = 0.101; not significant at 0.1
	8	—	—	—	—	—	—	
Trees								
controls	8	0.8	1.7	0.5	2.1	0.4	1.9	modified $t_7$ at = 2.714;
treated	8	0.5	7.7	0.4	8.4	0.3	7.2	significant at 0.05
<i>Prunus serotina</i>								
controls	8	0.0	1.3	0.0	1.2	0.0	1.1	modified $t_7$ at = 2.605;
treated	8	0.0	5.3	0.0	5.6	0.0	4.7	significant at 0.05
Other woody								
controls	8	0.0	20.8	0.0	8.6	0.0	3.9	$t_7$ at = 2.153; significant
treated	8	0.0	10.8	0.0	15.0	0.0	12.8	at 0.1
<i>Parthenocissus quinquefolia</i>								
controls	8	0.0	4.9	0.0	2.0	0.0	1.0	$t_7$ at = 2.193; significant
treated	8	0.0	4.8	0.0	4.8	0.0	3.7	at 0.1



TABLE 31. Comparison of herbs, trees, and other woody plants in natural understory *L. japonica* habitat by a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control (*L. japonica* unweeded) and treated (*L. japonica* weeded) plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Life Form		
	Trees	Other woody	Herbs
No. m <sup>2</sup> plots	8	8	3
Trans. mean differences	1.3	1.5	1.9
Duncan's 10% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance: The growth form mean square was smaller than the error mean square; therefore, not significant.

Bartlett's:  $\chi^2_{2 \text{ df}} = 1.064$ ; no significant variance at 0.1.

TABLE 32. Comparison of *Podophyllum peltatum* L. in the upland forest in exotic ground cover (*H. helix* and *L. japonica*) weeded (treated) and unweeded (control)  $1 \times 1$ -m plots by a paired plot design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data (no./m<sup>2</sup>)

Treatment	m <sup>2</sup> plot replications	Results						
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972	Corrected mean 1971	Corrected mean 1972	Significance
Unweeded	4	28.3	51.9	24.5	44.8	14.5	25.5	$t_3 \text{ df} = 1.274$ ;
Weeded	4	30.4	72.1	24.5	54.8	17.8	38.7	not significant at 0.1

TABLE 33. Comparison of herbaceous and woody plants in flood-plain *H. helix* weeded (treated) and unweeded (control)  $1 \times 1$ -m plots by paired plot design experiments (except herbs vs. woody which was a completely randomized design) on square root  $(\sqrt{x} + 0.5)$  transformed data (no./m<sup>2</sup>)

Experiments	m <sup>2</sup> plot replications	Results						Significance
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972	Corrected mean 1971	Corrected mean 1972	
Herbs								
controls	7	5.5	7.7	4.1	8.6	2.8	6.6	$t_6$ df = 2.445; significant at 0.1
treated	7	19.9	29.0	9.7	34.3	4.6	28.5	
<i>Impatiens capensis</i>								
controls	7	1.9	1.1	0.7	0.6	0.4	0.4	modified $t_6$ df = 1.462; not significant at 0.1
treated	7	1.3	2.3	0.7	1.9	0.5	1.4	
Other herbs								
controls	7	4.3	7.7	2.6	5.6	1.7	3.5	$t_6$ df = 0.954; not significant at 0.1
treated	7	10.5	17.6	5.6	10.1	2.8	6.2	
Woody								
controls	8	3.1	5.8	1.8	3.9	1.1	2.4	$t_7$ df = 0.775; not significant at 0.1
treated	8	2.1	6.6	1.0	5.1	0.6	3.5	
Herbs vs. woody	7	—	—	—	—	—	—	$t_{13}$ df = 1.643; not significant at 0.1
	8	—	—	—	—	—	—	
Trees								
controls	8	0.5	0.9	0.2	0.6	0.2	0.5	modified $t_7$ df = 0.885; not significant at 0.1
treated	8	0.4	3.6	0.1	1.9	0.1	1.1	
Other woody								
controls	8	1.4	4.3	0.5	2.5	0.3	1.5	$t_7$ df = 0.072; not significant at 0.1
treated	8	0.7	2.9	0.4	2.2	0.3	1.6	

TABLE 34. Comparison of herbs, trees, and other woody plants in flood-plain *H. helix* habitat by a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control (*H. helix* unweeded) and treated (*H. helix* weeded) plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Life Form		
	Other woody	Trees	Herbs
No. m <sup>2</sup> plots	8	8	7
Trans. mean differences	0.03	0.34	2.27
Duncan's 5% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{2/20 \text{ df}} = 4.125$ ; significant at 0.05.

Bartlett's:  $\chi^2_{2 \text{ df}} = 6.570$ ; significant variance at 0.05.

Biology: As shown by Duncan's test.



TABLE 35. Comparison of herbaceous and woody plants in cleared understory *L. japonica* weeded (treated) and unweeded (control)  $1 \times 1$ -m plots by paired plot design experiments on square root ( $\sqrt{x + 0.5}$ ) transformed data (no./m<sup>2</sup>)

Experiments	m <sup>2</sup> plot replications	Results						Significance
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972	Corrected mean 1971	Corrected mean 1972	
Herbs controls treated	10 10	12.0 15.9	34.7 82.5	17.9 22.5	41.9 110.9	15.7 19.7	34.2 96.7	$t_9$ at = 2.636 and modified $t_9$ at = 2.719; significant at 0.05 and 0.025 respectively
<i>Allium vineale</i> controls treated	10 10	8.3 12.7	32.7 50.8	13.6 16.8	36.3 35.1	12.0 14.9	27.9 21.5	$t_9$ at = 0.897; not significant at 0.1
<i>Oxalis stricta</i> controls treated	10 10	0.0 0.0	0.0 18.2	0.0 0.0	0.0 17.7	0.0 0.0	0.0 13.9	modified $t_9$ at = 4.764; significant at 0.005
Woody controls treated	10 10	0.4 1.3	35.4 42.0	0.2 1.1	51.4 58.2	0.2 0.9	46.4 51.4	$t_9$ at = 0.0003; not significant at 0.1
Herbs vs. woody	10 10	— —	— —	— —	— —	— —	— —	$t_9$ at = 1.941; significant at 0.1
Trees controls treated	10 10	0.4 1.1	1.3 8.5	0.2 0.7	0.7 13.5	0.2 0.5	0.5 12.4	modified $t_9$ at = 5.363; significant beyond 0.001

TABLE 35—continued

Experiments	m <sup>2</sup> plot replications	Results						Significance
		Standard deviation 1971	Standard deviation 1972	Mean no./m <sup>2</sup> 1971	Mean no./m <sup>2</sup> 1972	Corrected mean 1971	Corrected mean 1972	
<i>Liriodendron tulipifera</i>								
controls	10	0.0	0.0	0.0	0.0	0.0	0.0	modified $t_9$ at = 7.105; significant beyond 0.001
treated	10	0.0	3.4	0.0	5.0	0.0	4.6	
<i>Ulmus americana</i>								
controls	10	0.0	0.5	0.0	0.4	0.0	0.3	modified $t_9$ at = 4.491; significant at 0.005
treated	10	0.0	5.2	0.0	6.0	0.0	5.1	
Other woody								
controls	10	0.0	35.4	0.0	50.5	0.0	45.3	$t_9$ at = 0.824; not significant at 0.1
treated	10	0.0	40.2	0.0	43.8	0.0	33.3	
<i>Parthenocissus quinquefolia</i>								
controls	10	0.0	13.5	0.0	12.6	0.0	8.6	modified $t_9$ at = 0.939; not significant at 0.1
treated	10	0.0	5.5	0.0	6.0	0.0	4.8	
<i>Rhus radicans</i>								
controls	10	0.0	16.3	0.0	7.9	0.0	4.0	$t_9$ at = 0.610; not significant at 0.1
treated	10	0.0	9.3	0.0	4.3	0.0	2.2	
<i>Vitis rupestris</i>								
controls	10	0.0	29.6	0.0	26.5	0.0	19.7	$t_9$ at = 0.126; not significant at 0.1
treated	10	0.0	33.8	0.0	31.3	0.0	21.0	

TABLE 36. Comparison of herbs, trees, and other woody plants in cleared understory *L. japonica* habitat by a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control (*L. japonica* unweeded) and treated (*L. japonica* weeded) plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Life Form		
	Other woody	Trees	Herbs
No. m <sup>2</sup> plots	10	10	10
Trans. mean differences	-1.0	2.4	3.5
Duncan's 5% test			

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{2/27 \text{ df}} = 4.882$ ; significant at 0.025.

Bartlett's:  $\chi^2_{2 \text{ df}} = 9.569$ ; significant variance at 0.01.

Biology: Relative differences are as indicated by the transformed mean of the differences.

TABLE 40. Comparison of tree increase in different habitats after removal of exotic ground cover (*H. helix* and *L. japonica*) from a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control and treated plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Habitats			
	<i>H. helix</i> upland	<i>H. helix</i> flood plain	<i>L. japonica</i> natural understory	<i>L. japonica</i> cleared understory
No. m <sup>2</sup> plots	10	8	8	10
Trans. mean differences	0.33	0.34	1.28	2.38
Duncan's 10% test				

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/32 \text{ df}} = 7.019$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{3 \text{ df}} = 5.797$ ; no significant variance at 0.1.

TABLE 41. Comparison of woody plant (except trees) increase in different habitats after removal of exotic ground cover (*H. helix* and *L. japonica*) from a completely randomized design experiment on square root ( $\sqrt{x + 0.5}$ ) transformed data of the differences between control and treated plot readings in 1971 and 1972 (no./m<sup>2</sup>)

Characteristics	Habitats			
	<i>L. japonica</i> cleared understory	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> natural understory
No. m <sup>2</sup> plots	10	8	10	8
Trans. mean differences	-1.0	0.0	0.5	1.5
Duncan's 5% test				

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/32 \text{ df}} = 1.873$ ; not significant at 0.1.

Bartlett's:  $\chi^2_{3 \text{ df}} = 19.437$ ; significant variance beyond 0.001.

Biology: No differences between habitats.



TABLE 42. Comparison of swamp-marsh transition *I. pseudacorus* frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a paired (in time) plot (1 × 1 m) design survey

Comparisons	No. m <sup>2</sup> plots	Mean f/m <sup>2</sup>	Results	
			Heterogeneity $\chi^2$	$\chi^2$ test
Annual			$\chi^2_{12} \text{ df} = 12.746$	pooled $\chi^2_{1 \text{ df}} = 10.143$ ;
April 1971	13	93.2		significant at 0.005
April 1972	13	95.4	not significant at 0.1	
Spring			$\chi^2_{3 \text{ df}} = 194.758$	individual $\chi^2_{1 \text{ df}}$ ; 2
April 1972	4	98.2	significant beyond 0.001	significant beyond 0.001,
May 1972	4	86.0		2 not significant at 0.1
Spring-Summer I			$\chi^2_{3 \text{ df}} = 5358.914$ ;	individual $\chi^2_{1 \text{ df}}$ ; all
May 1972	4	86.0	significant beyond 0.001	4 significant beyond 0.001
August 1972	4	0.25		
Spring-Summer II			$\chi^2_{12 \text{ df}} = 10852.338$ ;	individual $\chi^2_{1 \text{ df}}$ ; 12
April 1972	13	95.4	significant beyond 0.001	significant beyond 0.001,
August 1972	13	15.0		1 not significant at 0.1

TABLE 43. Comparison of swamp-marsh transition *Peltandra virginica* frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a paired (in time) plot (1 × 1 m) design survey

Comparisons	No. m <sup>2</sup> plots	Mean f/m <sup>2</sup>	Results	
			Heterogeneity $\chi^2$	$\chi^2$ test
Annual				
April 1971	13	0.08	$\chi^2_{12}$ df = -64.770;	individual $\chi^2_{12}$ df; 12
April 1972	13	0.8	significant heterogeneity	not significant at 0.1, 1 significant beyond 0.001
Spring				
April 1972	4	1.2	$\chi^2_3$ df = -74.126;	individual $\chi^2_{12}$ df; 3
May 1972	4	6.5	significant heterogeneity	not significant at 0.1, 1 significant beyond 0.001
Spring-Summer I				
May 1972	4	6.5	$\chi^2_3$ df = 735.456;	individual $\chi^2_{12}$ df; 3
August 1972	4	38.2	significant beyond 0.001	significant beyond 0.001, 1 significant at 0.025
Spring-Summer II				
April 1972	13	0.8	$\chi^2_{12}$ df = -20155.133;	individual $\chi^2_{12}$ df; 6
August 1972	13	37.6	significant heterogeneity	significant beyond 0.001, 2 significant at 0.01, 1 significant at 0.05, 2 significant at 0.1, 2 not significant at 0.1

TABLE 44. Comparison of open marsh *Iris pseudacorus* frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a paired (in time) plot (1 × 1 m) design survey

Comparisons	Results		
	No. m <sup>2</sup> plots	Mean $f/m^2$	Heterogeneity $\chi^2$
Annual			$\chi^2$ test
April 1971	7	97.7	individual $\chi^2_{1 \text{ df}}$ ; 5
April 1972	7	81.3	significant beyond 0.001, 2 not significant at 0.1
Spring			individual $\chi^2_{1 \text{ df}}$ ; all
April 1972	3	82.3	3 significant beyond 0.001
June 1972	3	1.3	
Spring-Summer I			pooled $\chi^2_{1 \text{ df}}$ = 4.054; significant at 0.05
June 1972	3	1.3	
August 1972	3	0.0	
Spring-Summer II			individual $\chi^2_{1 \text{ df}}$ ; all
April 1972	7	81.3	7 significant beyond
August 1972	7	0.0	0.001

TABLE 45. Comparison of open marsh *Peltandra virginica* frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a paired (in time) plot (1 × 1 m) design survey

Comparisons	No. m <sup>2</sup> plots	Results		
		Mean f/m <sup>2</sup>	Heterogeneity $\chi^2$	$\chi^2$ test
Annual				
April 1971	7	0.0	$\chi^2_{6 \text{ df}} = 0.017$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 0.012$ ; not significant at 0.1
April 1972	7	0.4		
Spring				
April 1972	3	0.3	$\chi^2_{2 \text{ df}} = -324.753$ ; significant heterogeneity	individual $\chi^2_{1 \text{ df}}$ : 1 significant beyond 0.001, 2 not significant at 0.1
June 1972	3	6.7		
Spring-Summer I				
June 1972	3	6.7	$\chi^2_{2 \text{ df}} = 94.224$ ; significant beyond 0.001	individual $\chi^2_{1 \text{ df}}$ : 2 significant beyond 0.001, 1 significant at 0.01
August 1972	3	31.3		
Spring-Summer II				
April 1972	7	0.4	$\chi^2_{6 \text{ df}} = -27157.243$ ; significant heterogeneity	individual $\chi^2_{1 \text{ df}}$ : 6 significant beyond 0.001, 1 significant at 0.05
August 1972	7	46.0		

TABLE 46. Comparison of *Iris pseudacorus* in swamp-marsh transition with that of open marsh in frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a simple random sampling design survey, arc sine transformed before analysis

Comparisons	No. m <sup>2</sup> plots	Results			
		Standard deviation	Mean $\bar{f}/m^2$	Corrected mean	Significance
Marsh, April 1971 with transition, April 1972	7	2.3	97.7	98.3	$t_{18} \text{ df} = 0.792$ ;
	13	5.0	95.4	96.9	not significant at 0.1
Marsh, April 1972 with transition, May 1972	7	13.5	81.3	83.4	$t_9 \text{ df} = 0.585$ ;
	4	12.8	86.0	88.4	not significant at 0.1
Marsh, June 1972 with transition, August 1972	3	2.3	1.3	1.0	modified, $t' = 1.427$ ;
	13	29.6	15.0	7.9	not significant at 0.1
Marsh, August 1972 with transition, August 1972	7	0.0	0.0	0.2	modified, $t' = 1.966$ ;
	13	29.6	15.0	7.9	significant at 0.1



TABLE 47. Comparison of *Peltandra virginica* in swamp-marsh transition with that of open marsh in frequency per m<sup>2</sup> from a dm<sup>2</sup> grid by a simple random sampling design survey, arc sine transformed before analysis

Comparisons	No. m <sup>2</sup> plots	Results			Significance
		Standard deviation	Mean f/m <sup>2</sup>	Corrected mean	
Marsh, April 1972 with transition, April 1972	7	0.5	0.4	0.5	modified, $t' = 0.443$ ;
	13	1.6	0.8	0.6	not significant at 0.1
Marsh, June 1972 with transition, May 1972	3	3.5	6.7	6.3	$t_5$ at = 0.031;
	4	1.9	6.5	6.4	not significant at 0.1
Marsh, August 1972 with transition, August 1972	7	28.7	46.0	45.0	$t_{18}$ at = 0.617;
	13	30.0	37.6	34.8	not significant at 0.1

TABLE 48. Comparison of *Iris pseudacorus* and *Peltandra virginica* seed germination and survival from 225 seeds each planted at random but not collected at random

Species	Results			
	No. germinated	Percent germinated	0.05 confidence limits (%)	Probability and significance
<i>I. pseudacorus</i>	75	33	27-40	$P < 0.000000000298$ ;
<i>P. virginica</i>	142	63	57-70	significant beyond 0.001

TABLE 49. The influence of *Acorus calamus* growth on *Iris pseudacorus* as determined by fresh weight gain in g (of *Iris*) from a  $5 \times 5$  Latin square design experiment on logarithmic ( $\log(x+1)$ ) transformed data

Characteristics	Treatments			
	All <i>Acorus</i>	2/3 <i>Acorus</i>	1/2 <i>Acorus</i>	1/3 <i>Acorus</i> No <i>Acorus</i>
Original mean	0.0	404.4	531.1	687.5 1190.0
Adjusted transformed mean	-0.333	2.652	2.791	2.926 3.196
Duncan's 5% test				
Duncan's 1% test				
Corrected mean	-0.5	447.5	617.0	841.7 1570.6

Note: see Table 2 for note regarding Duncan's test.

Analysis of covariance:  $F_{4/111} \text{ at } = 4.565$ ; significant at 0.025.Bartlett's:  $\chi^2_{4 \text{ at for log of initial weight}} = 7.130$ ; no significant variance at 0.1.Bartlett's:  $\chi^2_{4 \text{ at for log of final weight}} = 2.682$ ; no significant variance at 0.1.TABLE 50. The influence of *Iris pseudacorus* growth on *Acorus calamus* as determined by fresh weight gain in g (of *Acorus*) from a  $5 \times 5$  Latin square design experiment on logarithmic ( $\log(x+1)$ ) transformed data

Characteristics	Treatments			
	All <i>Iris</i>	2/3 <i>Iris</i>	1/2 <i>Iris</i>	1/3 <i>Iris</i> No <i>Iris</i>
Original mean	0.0	180.9	266.7	365.6 550.5
Adjusted transformed mean	0.555	2.178	2.288	2.406 2.536
Corrected mean	2.6	149.6	193.1	253.5 342.2

Analysis of covariance:  $F_{4/111} \text{ at } = 3.127$ ; not significant at 0.05.Bartlett's:  $\chi^2_{4 \text{ at for log of initial weight}} = 7.629$ ; no significant variance at 0.1.Bartlett's:  $\chi^2_{4 \text{ at for log of final weight}} = 7.674$ ; no significant variance at 0.1.

TABLE 51. Comparison of light by percent of open sunlight in forested habitats on 23 September 1971, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats					
	Forest, no exotics	Flood plain, no exotics	<i>L. japonica</i> natural understory	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> cleared understory
No. of stations	10	10	8	8	10	10
Mean percent	23.3	37.7	39.7	41.8	43.6	78.8
Arc Sine mean	28.5	37.7	39.0	40.2	41.3	63.2
Duncan's 1% test	—	—	—	—	—	—
Duncan's 0.1% test	—	—	—	—	—	—
Corrected mean	22.7	37.4	39.6	41.7	43.6	79.6

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5,50 \text{ df}} = 38.200$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{3 \text{ df}} = 6.514$ ; no significant variance at 0.01.

TABLE 52. Comparison of light by percent of open sunlight in forested habitats on 7 November, 1971, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats					
	Forest, no exotics	<i>L. japonica</i> natural understory	<i>H. helix</i> upland	Flood plain, no exotics	<i>H. helix</i> flood plain	<i>L. japonica</i> cleared understory
No. of stations	10	8	10	10	8	10
Mean percent	49.1	62.3	63.8	64.8	70.0	92.2
Arc sine mean	44.5	52.2	53.2	53.9	56.9	75.0
Duncan's 1% test	—	—	—	—	—	—
Duncan's 0.1% test	—	—	—	—	—	—
Corrected mean	49.1	62.5	64.0	65.3	70.1	93.3

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5/150} \text{ at } = 29.905$ ; significant beyond 0.001.Bartlett's:  $\chi^2_5 \text{ at } = 8.642$ ; no significant variance at 0.01.



TABLE 53. Comparison of light by percent of open sunlight in forested habitats on 22 December, 1971, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats					
	Forest, no exotics	Flood plain, no exotics	<i>H. helix</i> flood plain	<i>H. helix</i> upland	<i>L. japonica</i> natural understory	<i>L. japonica</i> cleared understory
No. of stations	10	10	8	10	8	10
Mean percent	73.6	77.6	78.8	80.7	82.2	92.5
Arc sine mean	59.2	61.9	62.8	64.3	65.2	74.9
Duncan's 1% test						
Duncan's 0.1% test						
Corrected mean	73.9	77.8	79.1	81.3	82.4	93.3

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5,50} \text{ at } = 11.976$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_3 \text{ at } = 5.424$ ; no significant variance at 0.01.

TABLE 54. Comparison of light by percent of open sunlight in forested habitats on 4 February 1972, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats			
	Forest, no exotics	<i>H. helix</i> flood plain	<i>H. helix</i> upland	Flood plain, no exotics
No. of stations	10	8	10	10
Mean percent	80.4	83.3	84.8	85.9
Arc sine mean	64.0	66.1	67.7	68.2
Duncan's 1% test				
Duncan's 0.1% test				
Corrected mean	80.8	83.6	85.6	86.2
				87.8
				95.9

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5/50} \text{ at } = 6.917$ ; significant beyond 0.001.Bartlett's:  $\chi^2_5 \text{ at } = 6.354$ ; no significant variance at 0.01.

TABLE 55. Comparison of light by percent of open sunlight in forested habitats on 20 March 1972, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats				
	Flood plain, no exotics	<i>L. japonica</i> natural understory	<i>H. helix</i> upland	<i>H. helix</i> flood plain	Forest, no exotics
No. of stations	10	8	10	8	10
Mean percent	84.6	84.0	84.6	85.8	86.1
Arc sine mean	67.4	67.6	67.7	68.6	68.7
Duncan's 1% test					
Duncan's 0.5% test					
Corrected mean	85.3	85.5	85.6	86.7	86.8

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5,150 \text{ df}} = 4.032$ ; significant at 0.005.Bartlett's:  $\chi^2_{5 \text{ df}} = 3.056$ ; no significant variance at 0.01.*L. japonica*  
cleared  
understory

TABLE 56. Comparison of light by percent of open sunlight in forested habitats on 5 May 1972, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats					
	Forest, no exotics	Flood plain, no exotics	<i>L. japonica</i> natural understory	<i>H. helix</i> upland	<i>H. helix</i> flood plain	<i>L. japonica</i> cleared understory
No. of stations	10	10	8	10	8	10
Mean percent	60.1	68.1	75.5	78.3	80.3	92.0
Arc sine mean	50.9	55.8	60.8	62.4	64.5	75.7
Duncan's 1% test						
Duncan's 0.1% test						
Corrected mean	60.2	68.4	76.2	78.5	81.5	93.9

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5/150} \text{ at } = 14.619$ ; significant beyond 0.001.  
 Bartlett's:  $\chi^2_5 \text{ at } = 9.322$ ; no significant variance at 0.01.

TABLE 57. Comparison of light by percent of open sunlight in forested habitats on 30 June 1972, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats				
	Forest, no exotics	Flood plain, no exotics	<i>H. helix</i> upland	<i>L. japonica</i> natural understory	<i>H. helix</i> flood plain  <i>L. japonica</i> cleared understory
No. of stations	10	10	10	8	8
Mean percent	28.8	38.5	39.8	40.5	50.6
Arc sine mean	32.4	38.2	39.1	39.3	45.4
Duncan's 1% test					
Duncan's 0.1% test					
Corrected mean	28.7	38.3	39.7	40.1	50.6

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5,150} \text{ df} = 34.058$ ; significant beyond 0.001.Bartlett's:  $\chi^2_5 \text{ df} = 13.560$ ; no significant variance at 0.01.



TABLE 58. Comparison of light by percent of open sunlight in forested habitats on 7 August 1972, with and without *H. helix* and *L. japonica* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats					
	Forest, no exotics	<i>L. japonica</i> natural understory	Flood plain, no exotics	<i>H. helix</i> upland	<i>H. helix</i> flood plain	<i>L. japonica</i> cleared understory
No. of stations	10	8	10	10	8	10
Mean percent	22.1	38.3	41.4	44.1	49.0	73.0
Arc sine mean	27.7	38.1	40.0	41.6	44.4	58.9
Duncan's 1% test	—	—	—	—	—	—
Duncan's 0.1% test	—	—	—	—	—	—
Corrected mean	21.6	38.1	41.4	44.1	49.0	73.3

Note: see Table 2 for note regarding Duncan's test.

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{5/150} \text{ at } = 38.633$ ; significant beyond 0.001.Bartlett's:  $\chi^2_5 \text{ at } = 3.632$ ; no significant variance at 0.01.

TABLE 59. Comparison of light by percent of open sunlight in marsh habitats on 7 November 1971, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> swamp-marsh transition	<i>I. pseudacorus</i> marsh Marsh, no exotics
No. of stations	10	13	7
Mean percent	83.3	90.3	92.2
Arc sine mean	67.3	73.4	76.2
Duncan's 1% test			
Corrected mean	85.2	91.9	94.3

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/36} \text{ at } = 2.127$ ; not significant at 0.01.Bartlett's:  $\chi^2_3 \text{ at } = 2.008$ ; no significant variance at 0.01.

TABLE 60. Comparison of light by percent of open sunlight in marsh habitats on 22 December 1971, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> swamp-marsh transition	Marsh, no exotics  <i>I. pseudacorus</i> marsh
No. of stations	10	13	7
Mean percent	88.8	92.0	100.7
Arc sine mean	71.2	75.5	86.0
Duncan's 1% test			
Duncan's 0.5% test			
Corrected mean	89.6	93.7	99.5

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/36} \text{ at } = 5.601$ ; significant at 0.005.Bartlett's:  $\chi^2_3 \text{ at } = 4.008$ ; no significant variance at 0.01.

TABLE 61. Comparison of light by percent of open sunlight in marsh habitats on 4 February 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> swamp-marsh transition	Marsh, no exotics
No. of stations	10	13	10
Mean percent	93.8	95.6	98.6
Arc sine mean	77.9	78.8	81.9
Duncan's 1% test			83.2
Corrected mean	95.6	96.2	98.6

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3,36 \text{ df}} =$  the light percent mean square was smaller than the error mean square; therefore, not significant.  
 Bartlett's:  $\chi^2_{3 \text{ df}} = 3.132$ ; no significant variance at 0.01.

TABLE 62. Comparison of light by percent of open sunlight in marsh habitats on 20 March 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	<i>I. pseudacorus</i> swamp-marsh transition	Swamp-marsh transition, no exotics	Marsh, no exotics  <i>I. pseudacorus</i> marsh
No. of stations	13	10	7
Mean percent	94.3	93.4	99.8
Arc sine mean	77.2	77.7	84.9
Duncan's 1% test			
Corrected mean	95.1	95.4	99.2

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3,36} \text{ at } = 1.469$ ; not significant at 0.01.Bartlett's:  $\chi^2_3 \text{ at } = 1.762$ ; no significant variance at 0.01.



TABLE 63. Comparison of light by percent of open sunlight in marsh habitats on 5 May 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	Marsh, no exotics	<i>I. pseudacorus</i> swamp-marsh transition
No. of stations	10	10	13
Mean percent	97.4	97.1	100.0
Arc sine mean	79.8	80.1	83.5
Duncan's 1% test			
Corrected mean	96.9	97.0	98.7
			99.5

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/38} \text{ at } = 1.064$ ; not significant at 0.01Bartlett's:  $\chi^2_3 \text{ at } = 0.900$ ; no significant variance at 0.01.

TABLE 64. Comparison of light by percent of open sunlight in marsh habitats on 30 June 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	<i>I. pseudacorus</i> swamp-marsh transition	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> marsh Marsh, no exotics
No. of stations	13	10	7
Mean percent	92.1	94.8	104.5
Arc sine mean	75.7	79.1	87.5
Duncan's 1% test			
Duncan's 0.5% test			
Corrected mean	93.9	96.4	99.8

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/36}$  at = 5.248; significant at 0.005.Bartlett's:  $\chi^2_3$  at = 4.743; no significant variance at 0.01.

TABLE 65. Comparison of light by percent of open sunlight in marsh habitats on 7 August 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> swamp-marsh transition	<i>I. pseudacorus</i> marsh Marsh, no exotics
No. of stations	10	13	7
Mean percent	84.2	91.5	94.6
Arc sine mean	69.2	75.2	78.0
Duncan's 1% test			
Corrected mean	87.4	93.4	95.7

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/36} \text{ at } = 3.460$ ; not significant at 0.01.Bartlett's:  $\chi^2_3 \text{ at } = 6.722$ ; no significant variance at 0.01.

TABLE 66. Comparison of light oy percent of open sunlight in marsh habitats on 22 September 1972, with and without *I. pseudacorus* from simple random sampling design surveys on arc sine transformed data

Characteristics	Habitats		
	Swamp-marsh transition, no exotics	<i>I. pseudacorus</i> swamp-marsh transition	<i>I. pseudacorus</i> marsh Marsh, no exotics
No. of stations	10	13	7
Mean percent	87.2	94.2	98.8
Arc sine mean	71.1	79.3	85.7
Duncan's 1% test			
Duncan's 0.5% test			
Corrected mean	89.5	96.5	99.4

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3,36} \text{ at } = 5.425$ ; significant at 0.005.Bartlett's:  $\chi^2_3 \text{ at } = 5.452$ ; no significant variance at 0.01.

TABLE 67. Comparison of dry-weight biomass in g/m<sup>2</sup> with percent of open sunlight for *L. japonica* (both habitats) from regression design surveys

Characteristics	Total biomass from several years of growth	One year of biomass growth
Number of pairs	18	13
Equation	$Y_c = a + bX$	$Y_c = a + bX$
<i>Y</i> intercept (a)	-307.21468	-535.25128
Slope (b)	6.73884	8.46426
<i>t</i> value	16 df = 6.002	11 df = 5.427
Significance level	significant beyond 0.001	significant beyond 0.001
Coefficient of determination, $r^2$	69%	73%

Note: *Y* = biomass; *X* = light.

TABLE 68. Comparison of dry-weight biomass in g/m<sup>2</sup> with percent of open sunlight for *H. helix* (upland only) from regression design surveys

Characteristics	Total biomass from several years of growth	1 year of biomass growth
Number of pairs	10	10
Equation	$\log Y_c = \log a + b \log X$	$\log Y_c = \log a + X \log b$
<i>Y</i> intercept (a)	-1.47922	-0.38037
Slope (b)	2.25045	0.03424
<i>t</i> value	df 8 = 2.839	df 8 = 2.343
Significance level	significant at 0.025	significant at 0.05
Coefficient of determination, $r^2$	50%	41%

Note: *Y* = biomass; *X* = light.



TABLE 69. Comparison of chlorophyll in mg/g of dry-leaf weight to degree of shading in number of layers of cheesecloth from randomized block design experiments replicated three times each for *H. helix* and *L. japonica*

Experiments	Treatments				Significance at 0.1
	96 layers	48 layers	24 layers	12 layers	0 layers
<i>Hedera helix</i>					
Chlorophyll A					
SD	1.6	0.7	0.9	0.6	0.9
Mean mg/g	1.8	2.8	3.3	3.8	3.3
Chlorophyll B					
SD	1.1	0.6	0.7	0.6	0.2
Mean mg/g	1.3	2.2	2.3	2.4	2.0
Total Chlorophyll					
SD	2.7	1.3	1.6	1.2	1.0
Mean mg/g	3.1	5.0	5.5	6.2	5.2
<i>Lonicera japonica</i>					
Chlorophyll A					
SD	0.7	3.3	3.5	1.2	0.7
Mean mg/g	2.1	5.4	5.4	4.4	3.6
Chlorophyll B					
SD	0.8	2.6	3.4	1.2	0.5
Mean mg/g	2.5	4.8	5.5	4.1	3.1
Total Chlorophyll					
SD	1.4	5.9	6.8	2.4	1.2
Mean mg/g	4.6	10.2	10.9	8.5	6.6

Note: n.s. = not significant at 0.1;

 $\chi^2$  = Bartlett's chi-square test of homogeneity of variance;

Duncan's range test not shown because all analyses of variance are unmodified and not significant.

TABLE 70. Comparison of dry weight *H. helix* leaf biomass in g/dm<sup>2</sup> to degree of shading in number of layers of cheesecloth from a randomized block design experiment replicated three times

Characteristics	Treatments				
	96 layers	24 layers	48 layers	12 layers	0 layers
Standard deviation	0.08	0.08	0.11	0.04	0.03
Mean g/dm <sup>2</sup>	0.07	0.21	0.22	0.33	0.44
Duncan's 10% test	—	—	—	—	—
Duncan's 0.5% test	—	—	—	—	—

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{4/8 \text{ df}} = 9.176$ ; significant at 0.005.

Bartlett's:  $\chi^2_{4 \text{ df}} = 3.895$ ; no significant variance at 0.1.

TABLE 71. Comparison of dry-weight *L. japonica* leaf biomass in g/dm<sup>2</sup> to degree of shading in number of layers of cheesecloth from a randomized block design experiment replicated three times

Characteristics	Treatments				
	96 layers	48 layers	24 layers	12 layers	0 layers
Standard deviation	0.04	0.06	0.08	0.10	0.05
Mean g/dm <sup>2</sup>	0.06	0.09	0.12	0.24	0.39
Duncan's 10% test	—	—	—	—	—
Duncan's 0.1% test	—	—	—	—	—

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{4/8 \text{ df}} = 20.260$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{4 \text{ df}} = 2.235$ ; no significant variance at 0.1.

TABLE 72. Comparison of vigor of *H. helix* in cm<sup>2</sup> of green and chlorotic cover per dm<sup>2</sup> to degree of shading in number of layers of cheesecloth from a randomized block design experiment replicated three times

Characteristics	Treatments			
	96 layers	24 layers	48 layers	12 layers
Standard deviation	12.5	17.2	16.6	14.6
Mean cm <sup>2</sup> /dm <sup>2</sup>	12.3	38.7	44.3	86.3
Duncan's 10% test	—	—	—	—
Duncan's 1% test	—	—	—	—

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/6 \text{ df}} = 11.250$ ; significant at 0.01.

Bartlett's:  $\chi^2_{3 \text{ df}} = 0.241$ ; no significant variance at 0.1.

TABLE 73. Comparison of vigor of *L. japonica* in cm<sup>2</sup> of green and chlorotic cover per dm<sup>2</sup> to degree of shading in number of layers of cheesecloth from a randomized block design experiment replicated three times

Characteristics	Treatments				
	96 layers	48 layers	24 layers	12 layers	0 layers
Standard deviation	14.4	12.7	14.4	10.1	16.7
Mean cm <sup>2</sup> /dm <sup>2</sup>	8.3	13.7	33.3	76.3	85.0
Duncan's 10% test	—	—	—	—	—
Duncan's 0.1% test	—	—	—	—	—

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{4/8 \text{ df}} = 17.424$ ; significant beyond 0.001.

Bartlett's:  $\chi^2_{4 \text{ df}} = 0.536$ ; no significant variance at 0.1.

TABLE 74. Controlled shade regression experiments on *H. helix*

Experiments <sup>a</sup>	Results	
	No. of pairs	Equation
Chlorophyll A and shade	15	$Y_c = a + bX$
Chlorophyll B and shade	15	$Y_c = a + bX$
Total chlorophyll and shade	15	$Y_c = a + bX$
Leaf biomass and shade	15	$Y_c = a + b \log (X + 1)$
Vigor and shade	12	$Y_c = a + b \log (X + 1)$
Leaf biomass and vigor	15	$Y_c = a + bX$
Total chlorophyll and vigor	15	$Y_c = a + b \log (X + 1)$
Total chlorophyll and leaf biomass	15	$\log (Y + 1)_c = \log a + b \log (X + 1)$
Shade and light	15	$\log (Y + 1)_c = \log a + X \log b$
Chlorophyll A and light	15	$Y_c = a + b \log (X + 1)$
Chlorophyll B and light	15	$Y_c = a + b \log (X + 1)$
Total chlorophyll and light	15	$Y_c = a + b \log (X + 1)$
Leaf biomass and light	15	$Y_c = a + b \log (X + 1)$
Vigor and light	12	$Y_c = a + bX$

Note: See footnotes at end of table.

TABLE 74—*continued*

Experiments <sup>a</sup>	Results	
	Y intercept (a)	Slope (b)
Chlorophyll A and shade	3.66166	– 0.01819
Chlorophyll B and shade	2.34833	– 0.00875
Total chlorophyll and shade	5.96499	– 0.02680
Leaf biomass and shade	0.46580	– 0.17008
Vigor and shade	160.15292	–74.15674
Leaf biomass and vigor	0.04649	+ 0.00370
Total chlorophyll and vigor	2.39131	+ 1.63177
Total chlorophyll and leaf biomass	0.58889	+ 1.68898
Shade and light	1.73889	– 0.02663
Chlorophyll A and light	2.43429	+ 0.70967
Chlorophyll B and light	1.82987	+ 0.25226
Total chlorophyll and light	4.22967	+ 0.95510
Leaf biomass and light	0.13505	+ 0.14905
Vigor and light	27.32733	+ 2.62767



TABLE 74—continued

Experiments <sup>a</sup>	Results		
	<i>t</i> value	Significance	<i>r</i> <sup>2</sup> <sup>b</sup>
Chlorophyll A and shade	13 df = 2.591	significant at 0.025	34%
Chlorophyll B and shade	13 df = 1.750	not significant at 0.1	19%
Total chlorophyll and shade	13 df = 2.311	significant at 0.05	29%
Leaf biomass and shade	13 df = 5.654	significant beyond 0.001	71%
Vigor and shade	10 df = 4.574	significant at 0.005	68%
Leaf biomass and vigor	13 df = 8.287	significant beyond 0.001	84%
Total chlorophyll and vigor	13 df = 2.010	significant at 0.1	24%
Total chlorophyll and leaf biomass	13 df = 1.906	significant at 0.1	22%
Shade and light	13 df = 16.822	significant beyond 0.001	96%
Chlorophyll A and light	13 df = 2.016	significant at 0.1	24%
Chlorophyll B and light	13 df = 1.011	not significant at 0.1	7%
Total chlorophyll and light	13 df = 1.631	not significant at 0.1	17%
Leaf biomass and light	13 df = 4.587	significant beyond 0.001	62%
Vigor and light	10 df = 3.957	significant at 0.005	61%

<sup>a</sup>The dependent or *Y* variable is shown first in each pair, the *X* or independent variable is shown second. Chlorophyll is in mg/g of dry-leaf weight, shade is in layers of cheesecloth, leaf biomass is in g (dry weight)/dm<sup>2</sup>, vigor is in dm<sup>2</sup> of green and chlorotic leaves/dm<sup>2</sup>, and light is in percent of open sunlight.

<sup>b</sup>*r*<sup>2</sup> = coefficient of determination.

TABLE 75. Controlled shade regression experiments on *L. japonica*

Experiments <sup>a</sup>	Results	
	No. of pairs	Equation
Chlorophyll A and shade	15	$Y_c = a + bX$
Chlorophyll B and shade	15	$Y_c = a + bX$
Total chlorophyll and shade	15	$Y_c = a + bX$
Leaf biomass and shade	15	$Y_c = a + b \log (X + 1)$
Vigor and shade	15	$Y_c = a + b \log (X + 1)$
Leaf biomass and vigor	15	$Y_c = a + bX$
Total chlorophyll and vigor	15	$Y_c = a + b \log (X + 1)$
Total chlorophyll and leaf biomass	15	$Y_c = a + bX$
Shade and light	15	$\log (Y + 1)_c = \log a + X \log b$
Chlorophyll A and light	15	$Y_c = a + b \log (X + 1)$
Chlorophyll B and light	15	$Y_c = a + bX$
Total chlorophyll and light	15	$Y_c = a + bX$
Leaf biomass and light	15	$Y_c = a + bX$
Vigor and light	15	$Y_c = a + bX$

Note: See footnotes at end of table.

TABLE 75—*continued*

Experiments <sup>a</sup>	Results	
	Y intercept (a)	Slope (b)
Chlorophyll A and shade	4.86499	– 0.01902
Chlorophyll B and shade	4.42999	– 0.01194
Total chlorophyll and shade	9.26250	– 0.03006
Leaf biomass and shade	0.39825	– 0.17515
Vigor and shade	94.61634	–41.43184
Leaf biomass and vigor	0.03913	+ 0.00328
Total chlorophyll and vigor	7.90049	+ 0.20919
Total chlorophyll and leaf biomass	9.49581	– 7.25166
Shade and light	1.89724	– 0.02033
Chlorophyll A and light	3.93975	+ 0.23097
Chlorophyll B and light	4.21257	– 0.00655
Total chlorophyll and light	8.47860	– 0.00920
Leaf biomass and light	0.06246	+ 0.00366
Vigor and light	13.65661	+ 0.91510

TABLE 75—*continued*

Experiments <sup>a</sup>	Results		
	<i>t</i> value	Significance	<i>r</i> <sup>2</sup> <sup>b</sup>
Chlorophyll A and shade	13 df = 1.103	not significant at 0.1	9%
Chlorophyll B and shade	13 df = 0.750	not significant at 0.1	4%
Total chlorophyll and shade	13 df = 0.911	not significant at 0.1	6%
Leaf biomass and shade	13 df = 7.145	significant beyond 0.001	80%
Vigor and shade	13 df = 5.617	significant beyond 0.001	71%
Leaf biomass and vigor	13 df = 5.245	significant beyond 0.001	68%
Total chlorophyll and vigor	13 df = 0.128	not significant at 0.1	0.1%
Total chlorophyll and leaf biomass	13 df = 0.866	not significant at 0.1	5%
Shade and light	13 df = 17.914	significant beyond 0.001	96%
Chlorophyll A and light	13 df = 0.309	not significant at 0.1	1%
Chlorophyll B and light	13 df = 0.393	not significant at 0.1	1%
Total chlorophyll and light	13 df = 0.263	not significant at 0.1	1%
Leaf biomass and light	13 df = 7.511	significant beyond 0.001	81%
Vigor and light	13 df = 7.279	significant beyond 0.001	80%

<sup>a</sup>The dependent or *Y* variable is shown first in each pair, the *X* or independent variable is shown second. Chlorophyll is in mg/g of dry-leaf weight, shade is in layers of cheesecloth, leaf biomass is in g (dry weight)/dm<sup>2</sup>, vigor is in cm<sup>2</sup> of green and chlorotic leaves/dm<sup>2</sup>, and light is in percent of open sunlight.

<sup>b</sup>*r*<sup>2</sup> = coefficient of determination.

TABLE 76. Descriptive comparison of number of vegetational strata in different habitats from simple random sampling surveys

Vegetation	Strata			
	Overstory	Understory	Shrub	Tall herb Ground (low herb)
Forest, no exotics	X <sup>a</sup>	X	X	X
Upland <i>H. helix</i>	X	X	X	X
Natural understory <i>L. japonica</i>	X	X	X	X
Cleared understory <i>L. japonica</i>	X		X	X
Flood plain, no exotics	X	X	X	X
Flood-plain <i>H. helix</i>	X	X	X	X
Swamp-marsh transition, no exotics	X	X		X
Swamp-marsh transition <i>I. pseudacorus</i>	X		X	X
Swamp	X	X	X	X

<sup>a</sup>X = present.Upland forest (no exotics) comparison of tall herb height (mean of 0.218 m) with ground-layer height (0.124 m) each based on five samples:  $t_8$  at = 3.133; significant at 0.02.



TABLE 77. Correlation of ground layer heights in different but similar habitats from simple random sampling surveys

Characteristics	Flood plain habitats <sup>a</sup>		Upland habitats <sup>b</sup>		
	No exotic	<i>H. helix</i>	<i>H. helix</i>	<i>L. japonica</i> natural understory	<i>L. japonica</i> cleared understory
Number of samples	10	8	10	8	10
Mean height in m	0.057	0.056	0.060	0.071	0.124
Duncan's 5% test					0.138

Note: see Table 2 for note regarding Duncan's test.

<sup>a</sup> Modified  $t_{10}$  at  $r = 0.037$ ; not significant at 0.1.<sup>b</sup> Modified analysis of variance:  $F_{3/29}$  at  $r = 6.967$ ; significant at 0.005.

TABLE 78. The proportional number of strata present in each habitat compared with the expected number from the same habitat from simple random sampling design surveys

Surveys	No. of points	Proportion of strata present	Results	
			Heterogeneity $\chi^2$	$\chi^2$ test
Upland forest, no exotics	10	0.620	$\chi^2_{9 \text{ df}} = 2.18$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 7.22$ ; significant at 0.01
Upland <i>H. helix</i>	10	0.560	$\chi^2_{9 \text{ df}} = 1.12$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 9.68$ ; significant at 0.005
Natural understory <i>L. japonica</i>	8	0.525	$\chi^2_{7 \text{ df}} = 1.175$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 9.025$ ; significant at 0.005
Cleared understory <i>L. japonica</i>	10	0.600	$\chi^2_{9 \text{ df}} = 1.200$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 4.800$ ; significant at 0.05
Flood plain, no exotics	10	0.560	$\chi^2_{9 \text{ df}} = 0.32$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 9.68$ ; significant at 0.005
Flood-plain <i>H. helix</i>	8	0.650	$\chi^2_{7 \text{ df}} = 0.3$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 4.9$ ; significant at 0.05
Swamp-marsh transition, no exotics	10	0.575	$\chi^2_{9 \text{ df}} = 2.525$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 7.225$ ; significant at 0.01
Swamp-marsh transition <i>I. pseudacorus</i>	13	0.308	$\chi^2_{12 \text{ df}} = 2.576$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 24.923$ ; significant beyond 0.001
Swamp	13	0.385	$\chi^2_{12 \text{ df}} = 2.184$ ; not significant at 0.1	pooled $\chi^2_{1 \text{ df}} = 24.615$ ; significant beyond 0.001

TABLE 79. Significant associations of one stratum with another by pooled  $\chi^2$  from simple random sampling design surveys

Habitat	No. of points	Results		
		Stratum dependence		
		understory on overstory	tall herb on overstory	shrub on understory
All forests (5 layers)	59	$p^a = 0.05$ level $r^b = -0.70$		$p = 0.02$ level $r = -0.49$
Terrestrial forests (no swamp)	46			$p = 0.02$ level $r = -0.55$
Flood-plain forests	18		$p = 0.02$ level $r = -0.83$	

<sup>a</sup> $p$  = probability level; all shown are significant.<sup>b</sup> $r$  = tetrachoric coefficient of correlation.

TABLE 80. Some associations of one woody stratum depth (measured in m) with another by simple linear correlation from simple random sampling design surveys

Surveys <sup>a</sup>	Results			
	No. of pairs	Equation	<i>Y</i> intercept (a)	Slope (b)
Forest,				
no exotics	10	$Y_c = a + bX$		
shrub and understory			1.04290	-0.06949
shrub and overstory			0.73860	+0.00267
understory and overstory			6.80871	-0.21704
Upland				
<i>H. helix</i>	10	$Y_c = a + bX$		
shrub and understory			0.46584	+0.02148
shrub and overstory			0.70334	-0.00845
understory and overstory			11.20165	-0.40178
Natural				
understory	8	$Y_c = a + bX$		
<i>L. japonica</i>				
shrub and understory			0.77007	-0.21699
shrub and overstory			0.56339	-0.00258
understory and overstory			1.79410	-0.03189
Flood plain,				
no exotics	10	$Y_c = a + bX$		
shrub and understory			0.94213	-0.02572
shrub and overstory			0.96634	-0.01479
understory and overstory			8.45381	-0.12563

Note: See footnotes at end of table.

TABLE 80—continued

Surveys <sup>a</sup>	Results			
	No. of pairs	Equation	Y intercept (a)	Slope (b)
Flood-plain				
<i>H. helix</i>	8	$Y_c = a + bX$		
shrub and understory			2.90547	-0.28642
shrub and overstory			2.94176	-0.08884
understory and overstory			4.60829	+0.03599
Surveys <sup>a</sup>	Results			
	<i>t</i> value	Significance		$r^2$ <sup>b</sup>
Forest,				
no exotics				
shrub and understory	8 df = 1.197	not significant at 0.1		15%
shrub and overstory	8 df = 0.074	not significant at 0.1		0%
understory and overstory	8 df = 1.162	not significant at 0.1		14%
Upland				
<i>H. helix</i>				
shrub and understory	8 df = 0.330	not significant at 0.1		1%
shrub and overstory	8 df = 0.290	not significant at 0.1		1%
understory and overstory	8 df = 5.835	significant beyond 0.001		81%
Natural				
understory				
<i>L. japonica</i>				
shrub and understory	6 df = 1.092	not significant at 0.1		17%
shrub and overstory	6 df = 0.060	not significant at 0.1		0%
understory and overstory	6 df = 0.402	not significant at 0.1		3%



TABLE 80—continued

Surveys <sup>a</sup>	Results		
	<i>t</i> value	Significance	<i>r</i> <sup>2</sup> <sup>b</sup>
Flood plain, no exotics			
shrub and understory	8 df = 0.376	not significant at 0.1	2%
shrub and overstory	8 df = 0.524	not significant at 0.1	3%
understory and overstory	8 df = 0.895	not significant at 0.1	9%
Flood-plain <i>H. helix</i>			
shrub and understory	6 df = 3.318	significant at 0.02	65%
shrub and overstory	6 df = 1.440	not significant at 0.1	26%
understory and overstory	6 df = 0.179	not significant at 0.1	1%

<sup>a</sup>The dependent or *Y* variable is shown first in each pair, the *X* or independent variable is shown second.

<sup>b</sup>*r*<sup>2</sup> = coefficient of determination expressed in percent.

TABLE 81. Discriminant function applied to differentiation of habitats with *H. helix*, *L. japonica*, and *I. pseudacorus* and similar habitats without the exotic from depths of overstory, understory, and shrub layers in m from simple random sampling design surveys

Surveys	Results	
	No. of points	Discriminant function
Forest, no exotics with upland <i>H. helix</i>	20	$Z = X_1 + 1.2114 X_2 - 2.0954 X_3^a$ SHRUB, Understory, overstory <sup>b</sup>
Forest, no exotics with natural understory <i>L. japonica</i>	18	$Z = X_1 - 3.9982 X_2 - 13.1068 X_3$ SHRUB, Understory, overstory
Forest, no exotics with cleared understory <i>L. japonica</i>	20	$Z = X_1 + 6.5546 X_2 + 35.6655 X_3$ SHRUB, Understory, overstory
Flood plain with and without <i>H. helix</i>	18	$Z = 2.3231 X_1 + X_2 + 25.4955 X_3$ SHRUB, Overstory, understory
Swamp-marsh transition with and without <i>I. pseudacorus</i>	23	$Z = X_1 + 3.4253 X_2$ SHRUB and UNDERSTORY, overstory
Swamp and swamp-marsh transition (no exotics)	23	$Z = X_1 - 1.1911 X_2 + 3.8935 X_3$ SHRUB, Understory, overstory
Swamp and swamp-marsh transition ( <i>I. pseudacorus</i> )	26	$Z = 1.3379 X_1 + 4.1090 X_2 + X_3$ UNDERSTORY, Overstory, shrub

Surveys	Results	
	F value	Significance
Forest, no exotics with upland <i>H. helix</i>	more variation within groups than between groups	not significant
Forest, no exotics with natural understory <i>L. japonica</i>	3/14 df = 1.081	not significant at 0.1
Forest, no exotics with cleared understory <i>L. japonica</i>	3/16 df = 6.300	significant at 0.005
Flood plain with and without <i>H. helix</i>	more variation within groups than between groups	not significant
Swamp-marsh transition with and without <i>I. pseudacorus</i>	2/20 df = 8.216	significant at 0.005
Swamp and swamp-marsh transition (no exotics)	3/19 df = 9.133	significant beyond 0.001
Swamp and swamp-marsh transition ( <i>I. pseudacorus</i> )	3/22 df = 32.879	significant beyond 0.001

<sup>a</sup> $X_1$  is overstory,  $X_2$  is understory,  $X_3$  is shrub layer.

<sup>b</sup>The relative importance of each layer for each discriminant function is written in order with the most important on the left side.

TABLE 82. Relationship of living *Ulmus americana* overstory trees with *H. helix* and *L. japonica* from a census survey

Characteristics	Alive Standing <i>Ulmus americana</i>					Totals
	Exotic vines			Subtotal for exotic vines	No exotic vines	
	<i>H. helix</i> only	<i>L. japonica</i> only	<i>H. helix</i> and <i>L. japonica</i> (same tree)			
Number	79	23	2	104	83	187
Percent	42 <sup>a</sup>	12 <sup>a</sup>	1 <sup>a</sup>	56	44	100

<sup>a</sup> Due to rounding these three items add to 55.  
Note: More *U. americana* are infested by exotic vines [by 12 percent points (56% - 44% = 12%)] than are free.

Status of <i>U. americana</i>	Assumption of a Sample Instead of a Census	
	Percent	Confidence limits (% from a table)
Without exotics	44	0.05
With exotics	56	0.01
		36-53
		47-64

TABLE 83. Relationship of nonvigorous standing overstory trees (*U. americana* and all others) to *H. helix* and *L. japonica* vines from a census survey by cross-classification

Vigor of tree	Nonvigorous standing trees					
	<i>Ulmus americana</i>					
	<i>H. helix</i> only	<i>L. japonica</i> only	Both exotic vines on same tree	Subtotal for exotic vines	No exotic vines	Total for <i>Ulmus americana</i>
Dead	57% (60)	9% (9)	3% (3)	69% (72)	31% (33)	100% (105)
Dying	38% (12)	16% (5)	0% (0)	53% (17)	47% (15)	100% (32)
Both types	53% (72)	10% (14)	2% (3)	65% (89)	35% (48)	100% (137)

Vigor of tree	Nonvigorous standing trees					
	All others					
	<i>H. helix</i> only	<i>L. japonica</i> only	Both exotic vines on same tree	Subtotal for exotic vines	No exotic vines	Total for all others
Dead	34% (48)	8% (11)	1% (1)	42% (60)	58% (82)	100% (142)
Dying	35% (53)	6% (9)	0% (0)	41% (62)	59% (88)	100% (150)
Both types	35% (101)	7% (20)	0% (1)	42% (122)	58% (170)	100% (292)

Note: Some percents may not add to totals or subtotals due to rounding, absolute data in parentheses;

51% of all standing nonvigorous trees (*U. americana* and all others) have no exotics, 49% of all standing nonvigorous trees (*U. americana* and all others) have exotics; of this latter group

40% of all trees (*U. americana* and all others) have *H. helix* only,

8% of all trees (*U. americana* and all others) have *L. japonica* only,

1% of all trees (*U. americana* and all others) have both species.

TABLE 84. Tabular analysis of exotic vines with vigor and tree type from data of Table 83

Percent points difference between <i>U. americana</i> and others for both vigor types			
Dependent variable	Subtraction	Difference	
No exotic vines	58% - 35%	=	23% points
Exotic vines	65% - 42%	=	23% points
<i>H. helix</i>	53% - 35%	=	18% points
<i>L. japonica</i>	10% - 7%	=	3% points
Both species	2% - 0%	=	2% points

Stratification by vigor of tree			
Variables	Subtraction	Difference	Difference for both vigor types
Dead trees, no exotics	58% - 31%	=	27% points
Dead trees, exotics present	69% - 42%	=	27% points
Dead trees, <i>H. helix</i>	57% - 34%	=	23% points
Dead trees, <i>L. japonica</i>	9% - 8%	=	1% point
Dead trees, both species	3% - 1%	=	2% points
Dying trees, no exotics	59% - 47%	=	12% points
Dying trees, exotics present	53% - 41%	=	12% points
Dying trees, <i>H. helix</i>	38% - 35%	=	3% points
Dying trees, <i>L. japonica</i>	16% - 6%	=	10% points
Dying trees, both species	0% - 0%	=	0% point

	>		23% points	significant
	>		23% points	significant
	>		18% points	significant
	<		3% points	not significant
	=		2% points	not significant
	<		23% points	not significant
	<		23% points	not significant
	<		18% points	not significant
	>		3% points	significant
	<		2% points	not significant



TABLE 85. Relationship of overstory size down trees (*U. americana* and all others) and type of fall (cut or natural) to *Hedera helix* and *Lonicera japonica* vines from a census survey by cross-classification

Type of fall	Down trees			
	<i>Ulmus americana</i>			
	<i>Hedera</i> before fall	<i>Hedera</i> after fall	<i>Lonicera</i> before fall	<i>Lonicera</i> after fall
Natural	2% (1)	15% (7)	2% (1)	17% (8)
Cut	0% (0)	32% (30)	0% (0)	20% (19)
Both types	— (1)	— (37)	— (1)	— (27)

Type of fall	Down trees			
	<i>Ulmus americana</i>			
	<i>Lonicera</i> before <i>Hedera</i> after fall	Both species after fall	<i>Hedera</i> before both species after fall	<i>Hedera</i> after both species before fall
Natural	0% (0)	2% (1)	0% (0)	0% (0)
Cut	0% (0)	7% (7)	0% (0)	0% (0)
Both types	— (0)	— (8)	— (0)	— (0)

Type of fall	Down trees				
	<i>Ulmus americana</i>				
	<i>Hedera</i> before and after fall	<i>Lonicera</i> before and after fall	Subtotal for exotic vines	No exotic vines	Total for <i>Ulmus americana</i>
Natural	11% (5)	7% (3)	57% (26)	43% (20)	100% (46)
Cut	5% (5)	0% (0)	65% (61)	35% (33)	100% (94)
Both types	— (10)	— (3)	— (87)	— (53)	— (140)

Note: Some percents may not add to totals or subtotals due to rounding, absolute data in parentheses.

TABLE 85—*continued*

Type of fall	Down trees			
	All others			
	<i>Hedera</i> before fall	<i>Hedera</i> after fall	<i>Lonicera</i> before fall	<i>Lonicera</i> after fall
Natural	1% (3)	28% (99)	1% (4)	8% (28)
Cut	0% (0)	21% (4)	5% (1)	16% (3)
Both types	1% (3)	27% (103)	1% (5)	8% (31)

Type of fall	Down trees			
	All others			
	<i>Lonicera</i> before <i>Hedera</i> after fall	Both species after fall	<i>Hedera</i> before both species after fall	<i>Hedera</i> after both species before fall
Natural	0% (1)	1% (3)	0% (1)	0% (1)
Cut	0% (0)	5% (1)	0% (0)	0% (0)
Both types	0% (1)	1% (4)	0% (1)	0% (1)

Type of fall	Down trees				
	All others				
	<i>Hedera</i> before and after fall	<i>Lonicera</i> before and after fall	Subtotal for exotic vines	No exotic vines	Total for all others
Natural	8% (29)	2% (7)	49% (176)	51% (181)	100% (357)
Cut	0% (0)	0% (0)	47% (9)	53% (10)	100% (19)
Both types	8% (29)	2% (7)	49% (185)	51% (191)	100% (376)

Note: Some percents may not add to totals or subtotals due to rounding, absolute data in parentheses.

TABLE 86. Percent of all down trees (*Ulmus americana* and all others) with various types of *H. helix* and *L. japonica* infestation from data of Table 85

Percent	Type of infestation
47	No exotic vines
53	Have exotic vines
1	<i>H. helix</i> before fall
27	<i>H. helix</i> after fall
1	<i>L. japonica</i> before fall
11	<i>L. japonica</i> after fall
0	<i>L. japonica</i> before, <i>H. helix</i> after fall
2	Both species after fall
0	<i>H. helix</i> before, both after fall
0	<i>H. helix</i> after, both before fall
8	<i>H. helix</i> before and after fall
2	<i>L. japonica</i> before and after fall

TABLE 87. Tabular analysis of exotic vines with type of tree fall and tree type from data of Table 85

Dependent variable	Percent points difference between <i>U. americana</i> and others for both fall types	
	Subtraction	Difference
No exotic vines	51% - 38%	13% points
Exotic vines	62% - 49%	13% points
<i>H. helix</i> before fall	1% - 1%	0% point
<i>H. helix</i> after fall	27% - 26%	1% point
<i>L. japonica</i> before fall	1% - 1%	0% point
<i>L. japonica</i> after fall	19% - 8%	11% points
<i>L. japonica</i> before, <i>H. helix</i> after	0% - 0%	0% point
Both species after fall	6% - 1%	5% points
<i>H. helix</i> before, both species after	0% - 0%	0% point
<i>H. helix</i> after, both species before	0% - 0%	0% point
<i>H. helix</i> before and after fall	8% - 7%	1% point
<i>L. japonica</i> before and after fall	2% - 2%	0% point

TABLE 88. Tabular analysis of exotic vines with tree fall type and tree type from data of Table 85

Variables	Stratification by type of tree fall				Difference for both fall types	Significance
	Subtraction	Difference				
Natural fall, no exotics	51% - 43%	=	8% points	<	13% points	not significant
Natural fall, exotics present	57% - 49%	=	8% points	<	13% points	not significant
Natural fall, <i>H. helix</i> before	2% - 1%	=	1% point	>	0% point	significant
Natural fall, <i>H. helix</i> after	28% - 15%	=	13% points	>	1% point	significant
Natural fall, <i>L. japonica</i> before	2% - 1%	=	1% point	>	0% point	significant
Natural fall, <i>L. japonica</i> after	17% - 8%	=	9% points	<	11% points	not significant
Natural fall,						
<i>L. japonica</i> before <i>H. helix</i> after	0% - 0%	=	0% point	=	0% point	not significant
Natural fall, both species after	2% - 1%	=	1% point	<	5% points	not significant
Natural fall,						
<i>H. helix</i> before, both after	0% - 0%	=	0% point	=	0% point	not significant
Natural fall,						
<i>H. helix</i> after, both before	0% - 0%	=	0% point	=	0% point	not significant
Natural fall,						
<i>H. helix</i> before and after	11% - 8%	=	3% points	>	1% point	significant
Natural fall,						
<i>L. japonica</i> before and after	7% - 2%	=	5% points	>	0% point	significant
Cut fall, no exotics	53% - 35%	=	18% points	>	13% points	significant
Cut fall, exotics present	65% - 47%	=	18% points	>	13% points	significant
Cut fall, <i>H. helix</i> before	0% - 0%	=	0% point	=	0% point	not significant
Cut fall, <i>H. helix</i> after	32% - 21%	=	11% points	>	1% point	significant
Cut fall, <i>L. japonica</i> before	5% - 0%	=	5% points	>	0% point	significant
Cut fall, <i>L. japonica</i> after	20% - 16%	=	4% points	<	11% points	not significant
Cut fall,						
<i>L. japonica</i> before <i>H. helix</i> after	0% - 0%	=	0% point	=	0% point	not significant
Cut fall, both species after	7% - 5%	=	2% points	<	5% points	not significant



Cut fall, <i>H. helix</i> before, both after	0% – 0%	=	0% point	=	0% point	not significant
Cut fall, <i>H. helix</i> after, both before	0% – 0%	=	0% point	=	0% point	not significant
Cut fall, <i>H. helix</i> before and after	5% – 0%	=	5% points	>	1% point	significant
Cut fall, <i>L. japonica</i> before and after	0% – 0%	=	0% point	=	0% point	not significant

TABLE 89. Comparison of elevations in the open marsh and swamp-marsh transition zone in meters from a simple random sampling design survey

Comparisons	Results		
	No. of points	Standard deviation	Mean m/point
Tree line stations with bank stations	10	0.087	0.715
Head of gut stations with mouth of gut stations	10	0.124	0.566
	10	0.080	0.680
	10	0.160	0.600
			Significance
			$t_{18} \text{ at } = 3.111$ ;
			significant at 0.01
			(modified) $t' = 1.413$ ;
			not significant at 0.1

TABLE 90. Comparison of topographic elevations in meters in the open marsh and swamp-marsh transition zone with and without *I. pseudacorus* from simple random sampling design surveys

Characteristics	Habitats		
	Marsh, no exotics	<i>I. pseudacorus</i> marsh	Swamp-marsh transition, no exotics
No. of sampling points	10	7	10
Standard deviation	0.130	0.024	0.087
Mean elevation, m/point	0.573	0.691	0.715
Duncan's 0.5% test			13
			0.025
			0.784

Note: see Table 2 for note regarding Duncan's test.

Analysis of variance:  $F_{3/36} \text{ at } = 13.327$ ; significant beyond 0.001.Bartlett's:  $\chi^2_3 \text{ at } = 32.804$ ; significant variance beyond 0.001.Physical conditions: *Iris* areas are higher than their non-*Iris* counterparts as shown by mean elevations.

TABLE 91. Comparison of dry-weight biomass in g/m<sup>2</sup> with percent of open sunlight and topographic elevation (in m) for *I. pseudacorus* from a regression design survey of 20 points

Characteristics <sup>a</sup>	Multiple regression <sup>b</sup>	Simple regression, biomass and light	Simple regression, biomass and elevation
Equation	$Y_c = a + b_1X_1 + b_2X_2$	$Y_c = a + bX$	$Y_c = a + bX$
Y intercept (a)	-696.18234	5821.99883	-3818.23869
Slope (b)	$b_1$ -23.99642 $b_2$ 5056.64505	-52.43042	6157.98561
F or t value	$F_{2/17} \text{ df} = 8.906$	$t_{18} \text{ df} = 2.627$	$t_{18} \text{ df} = 3.984$
significance level	significant at 0.005	significant at 0.02	significant beyond 0.001
$R^2$ or $r^2$	$R^2_{Y,12} = 51\%$	$r^2 = 28\%$	$r^2 = 47\%$
$r^2_{Y2,1}$	32%		
t value for $r^2_{Y2,1}$	$t_{17} \text{ df} = 2.857$		
significance $r^2_{Y2,1}$	significant at 0.02		
$r^2_{Y1,2}$	8%		
t value for $r^2_{Y1,2}$	$t_{17} \text{ df} = 1.224$		
significance $r^2_{Y1,2}$	not significant at 0.1		

<sup>a</sup> $R^2$  = coefficient of multiple determination expressed as a percent; $r^2$  = coefficient of determination expressed as a percent.<sup>b</sup> $Y$  = biomass in g/m<sup>2</sup>; $X_1$  = percent of open sunlight; $X_2$  = topographic elevation in m.

TABLE 92. Comparisons of presence or absence of *Peltandra virginica* in four microvegetation types by  $\chi^2$  analysis in  $2 \times 2$  contingency tables from simple random sampling design surveys

Vegetation comparisons	Results		
	No. of points	$\chi^2$	Significance
<i>I. pseudacorus</i> areas (marsh and transition) with similar but non- <i>Iris</i> areas	40	1.758	not significant at 0.1
Marshes with and without <i>I. pseudacorus</i>	17	2.299	not significant at 0.1
Swamp-marsh transitions with and without <i>I. pseudacorus</i>	23	0.212	not significant at 0.1
Marshes with the swamp-marsh transitions	40	0.001	not significant at 0.1
			$r_{\text{tet}}^a$
			-0.34
			-0.61
			-0.16
			+0.01

<sup>a</sup>Tetrachoric coefficient of correlation.

TABLE 93. Comparisons of soil color (mostly gley or mostly not gley) in the upper 20 cm in four vegetation types by  $\chi^2$  analysis and exact probabilities in  $2 \times 2$  contingency tables from simple random sampling design surveys

Vegetation Comparisons	Results		
	No. of points	$\chi^2$ or $p^a$	Significance
<i>I. pseudacorus</i> areas (marsh and transition) with similar but non- <i>Iris</i> areas	39	2.438	not significant at 0.1
Marshes with and without <i>I. pseudacorus</i>	17	0.092	not significant at 0.1
Swamp-marsh transitions with and without <i>I. pseudacorus</i>	22	$p = 0.074$	significant at 0.07
Marshes with the swamp-marsh transitions	39	1.010	not significant at 0.1

<sup>a</sup> $p$  is exact probability; transition *Iris* is associated with gley.<sup>b</sup> $r_{tet}$  is tetrachoric coefficient of correlation.



TABLE 94. Comparisons of presence or absence of soil hardpan in the upper 20 cm in four vegetation types by  $\chi^2$  analysis in  $2 \times 2$  contingency tables from simple random sampling design surveys

Vegetation Comparisons	No. of points	$\chi^2$ or $\chi^2_{\text{Y}}^{\text{a}}$	Results		$r_{\text{tet}}^{\text{b}}$
			Significance		
<i>I. pseudacorus</i> areas (marsh and transition) with similar but non- <i>Iris</i> areas	39	<sup>a</sup> 4.418	significant at 0.05; <i>Iris</i> associated with hardpan		+ 0.59
Marshes with and without <i>I. pseudacorus</i>	17	0.004	not significant at 0.1		+ 0.03
Swamp-marsh transitions with and without <i>I. pseudacorus</i>	22	<sup>a</sup> 8.814	significant at 0.005 <i>Iris</i> associated with hardpan		+ 0.92
Marshes with the swamp-marsh transitions	39	1.042	not significant at 0.1		+ 0.27

<sup>a</sup> $\chi^2_{\text{Y}}$  is  $\chi^2$  with Yates' correction.<sup>b</sup> $r_{\text{tet}}$  is tetrachoric coefficient of correlation.

TABLE 95. Comparison of total water discharge (cfs) of the Potomac River during the growing season

a. April through September 1962 through 1971		
	Years	Total Discharge
	1962 and 1963	2,156,892
	1964 and 1965	2,189,792
	1966 and 1967	2,472,975
	1968 and 1969	2,042,270
	1970 and 1971	3,682,550
b. March through June 1971 and 1972		
Month	1971	1972
March	663,700	851,500
April	322,800	744,780
May	475,640	775,400
June	456,210	1,472,560
	Total	1,918,350
	Mean	479,587.5
	$t_{6 \text{ df}} = 2.592$ , significant at 0.05	

TABLE 96. Miscellaneous observations

Observations	Date
<i>L. japonica</i> does not occur in the swamp but does occur on the flood plain	March 1971
<i>H. helix</i> does not occur in the swamp	April 1971
Dead <i>L. japonica</i> stems found under upland <i>H. helix</i> in three plots	16 April 1971
Several <i>I. pseudacorus</i> rhizomes found with chunks missing as though they had been partially eaten	May and June 1971
<i>I. pseudacorus</i> seedlings (2) found in two flood plain <i>H. helix</i> plots, but did not survive	25 June 1971
<i>I. pseudacorus</i> seed germinating before falling from capsule	13 October 1971
Many <i>Acorus calamus</i> rhizomes were found growing on top of dead <i>Iris pseudacorus</i> rhizomes	10 April 1972
During the competition experiment 20 of 75 <i>I. pseudacorus</i> plants flowered (27%); and 4 of 75 <i>A. calamus</i> plants flowered (5%)	May and June 1972
<i>I. pseudacorus</i> seedlings (2) found in one flood plain <i>H. helix</i> plot [same block as one of above plots 25 June 1971], but did not survive	18 May 1972 and 15 August 1972
Mature <i>I. pseudacorus</i> plants found growing on fill gravel in several places on causeway to island and in one place on island, all above or at limit of high tide	Spring 1972
Understory trees in swamp-marsh transition without <i>I. pseudacorus</i> were <i>Salix caroliniana</i>	12 June 1972
Down logs of <i>Ulmus americana</i> do not have tightly adhering bark	October 1972
Growth ring counts of two overstory sized down <i>Robinia pseudo-acacia</i> trees covered with <i>H. helix</i> before the fall and ring counts of the vine at same level: (1) mean of 0.27 cm/ring for 33 inner rings and 0.16 cm/ring for 16 outer rings; <i>H. helix</i> , 21 rings (8.4 m from base of tree); (2) mean of 0.48 cm/ring for 13 inner rings and 0.22 cm/ring for 21 outer rings; <i>H. helix</i> , 25 rings (0.9 m from base of tree)	17 October 1972
Largest <i>L. japonica</i> vine found on Little Island: 7.3 mm dbh (average of two readings) with nine growth rings	19 October 1973
Largest <i>H. helix</i> vine found on Little Island: 12.5 mm dbh (average of two readings) with seven growth rings	19 October 1973

TABLE 97. Comparison of three methods of determining dominance and rate of growth on *H. helix*, *I. pseudacorus*, and *L. japonica*. (Tables consulted for data shown in parentheses.)

Comparisons	Method and results shown by that method		
	Biomass (B)	Frequency (F)	Cover (C)
Dominance—from Tables 2, 3, and 4	not comparable (cf with F or C (Table 2))	not comparable (cf with B or C (Table 3))	not comparable (cf with B or F (Table 4))
Rate of growth			
Upland <i>Hedera</i>			
Control and 1 yr		cf with C (Table 8)	cf with F (Table 19)
Control and 1.25 yr		not cf with C (Table 8)	not cf with F (Table 19)
1 yr and 1.25 yr	cf with original F, but not C (Table 5)	original F cf with B transformed F cf with C (Table 8)	cf with transformed F, but not B (Table 19)
Flood-plain <i>Hedera</i>			
Control and 1 yr		cf with C (Table 11)	cf with F (Table 20)
Control and 1.25 yr		cf with C (Table 12)	cf with F (Table 20)
1 and 1.25 yr	cf with F and C (Table 5)	cf with B and C (Table 13)	cf with B and F (Table 20)
Natural <i>Lonicera</i>			
Control and 1 yr			
Control and 1.25 yr			
1 and 1.25 yr	cf with F (Table 5)	cf with B (Tables 9 & 10)	
Cleared <i>Lonicera</i>			
Control and 1 yr			
Control and 0.25 yr			
1 yr and 0.25 yr	not cf with F (Table 5)	not cf with B (Table 16)	

TABLE 97.—*continued*

Comparisons	Method and results shown by that method		
	Biomass (B)	Frequency (F)	Cover (C)
Different habitats			
1 year	cf with C and transformed F (Table 6)	transformed F cf with B or C (Table 17)	cf with B, and transformed F (Table 21)
1.25 yr	cf with C, but not F (Table 7)	cf with C, but not B (Table 18)	cf with B and F (Table 22)

Biomass gives the same result as frequency in four out of seven cases. Two of the four cases are somewhat questionable since comparability is only with original frequency, or with transformed frequency.

Biomass gives the same result as cover in three out of five cases.

Cover gives the same result as frequency in seven out of nine cases. Two of the seven cases are somewhat questionable since comparability is only with transformed frequency.



# References

- ANDERSON, R. F. 1964. Forest and Shade Tree Entomology. Second printing. John Wiley and Sons, Inc., New York. 428 p.
- ARNON, D. I. 1949. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in *Beta vulgaris*. *Plant Physiol.* 24:1-15.
- ATANASIU, L. 1965. Despre unele fenomene fiziologice la citeva plante perene sem-pervirente si cereale de toamna, in decursul iernii [About some physiological phenomena in several evergreen perennials or trees and in wintering cereals during winter.] *Analele Universitatii Bucuresti Seria Stiintele Naturii i Matematica-Mecanica* 14:93-108 (Biological Abstracts, 1967, #108486).
- BILLINGS, W. D. 1970. Plants, Man, and the Ecosystem, Second edition. Wadsworth Publishing Company, Inc., Belmont, California. 160 p.
- BOYCE, J. S. 1948. Forest Pathology. Second edition. McGraw-Hill Book Co., Inc., New York. 550 p.
- CHICK, W. D., JR. 1966. (May 4). Memorandum to Superintendent, PWFP-GWMP from Regional Chief, Division of Interpretation and Resources Management. Subject: Trees infected with Dutch elm disease on Theodore Roosevelt Island. Y22-NCR (OIR).
- CODY, W. J. 1961. *Iris pseudacorus* L. escaped from cultivation in Canada. *Can. Field Nat.* 75(3):139-142.
- COLLINGWOOD, G. H., AND W. D. BRUSH. 1955. Knowing Your Trees (51 tree edition). Fifteenth printing. The American Forestry Association, Washington, D.C. 110 p.
- DAUBENMIRE, R. F. 1965. Plants and Environment. Second edition, fourth printing. John Wiley and Sons, Inc., New York. 422 p.
- DUHAMEL, J. F. 1935. Analostan Island. Records of the Columbia Historical Soc. Washington, D.C. 35-36:133-145.
- EDLIN, H. L. 1970. Woodland notebook: evergreen broadleaves. *Q. J. For.* 64 (1):49-59.
- ELTON, C. S. 1958. The Ecology of Invasions by Animals and Plants. Chapman and Hall, London. 181 p.
- ESAU, K. 1965. Plant Anatomy. Second edition. John Wiley and Sons, Inc., New York. 767 p.
- FASSETT, N. C. 1940. A Manual of Aquatic Plants. First edition. McGraw-Hill Book Co., Inc., New York. 382 p.
- FERNALD, M. L. 1950. Gray's Manual of Botany. Eighth edition. American Book Company, New York. 1632 p.
- FOWELLS, H. A. 1965. Silvics of Forest Trees of the United States. Agriculture Handbook No. 271. United States Department of Agriculture. United States Government Printing Office, Washington, D.C. 762 p.
- FRIEND, D. T. C. 1961. A simple method of measuring integrated light values in the field. *Ecology* 42:577-580.
- GADGIL, M., AND O. T. SOLBRIG. 1972. The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. *Am. Nat.* 106(947):14-31.
- GEIDEMAN, T. S., AND G. P. SIMONOV. 1971. Novaya assotsiatsiya v grabinnikovoi dubrave [A new association in hornbeam [*Carpinus*] oakwoods]. *Akademiia nauk Moldavskoi SSR Ki-Shihevi Izvestiia Serii Biologiches-Kikh i Khimicheskikh nauk* 1:83-84.
- GILLHAM, M. E. 1957. Coastal vegetation of Mull and Iona in relation to salinity and soil reaction. *J. Ecol.* 45(3):757-778.
- GILLULY, J., A. C. WATERS, AND A. O. WOODFORD. 1955. Principles of Geology. W. H. Freeman and Company, San Francisco. 631 p.
- GLEASON, H. A. 1952. The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada.

- The New York Botanical Garden, Lancaster Press, Inc., Lancaster, Penna. 3 vol.
- GRASOVSKY, A. 1929. Some aspects of light in the forest. Yale University School of Forestry Bull. No. 23. 53 p.
- GUNNING, B. A. 1964. Controlling honeysuckle in hedges. *N. Z. J. Agric.* **108**(4):330.
- HANDLEY, C. O. 1945. Japanese honeysuckle in wildlife management. *J. Wildl. Manage.* **9**(4):261-264.
- HARLOW, W. M., AND E. S. HARRAR. 1950. Textbook of Dendrology. Third edition. McGraw-Hill Book Company, Inc., New York. 555 p.
- HITCHCOCK, A. S., AND P. C. STANDLEY. 1919. Flora of the District of Columbia and vicinity. Contributions from the United States National Herbarium, vol. 21. 329 p.
- HOUGH, R. B. 1936. Handbook of the Trees of the Northern States and Canada East of the Rocky Mountains. Fifth printing. Romeyn B. Hough Company, Lowville, New York. 470 p.
- KARTASCHOFF, R. 1958. Die Keimverzögerung der Samen von *Iris Pseudacorus* L. (The retardation of the germination of seeds of *Iris pseudacorus* L.). *Ber. Schweiz. Bot. Ges.* **68**:145-182.
- KASSAS, M. 1952. Studies in the ecology of Chippenham fen. III. The forty acre wood. *J. Ecol.* **40**(1):50-61.
- KEPHART, L. W. 1939. The eradication of wild honeysuckle. United States Department of Agriculture, Bureau of Plant Industry. National Agricultural Library Call Number 1.9, P6917 Ewh. 3 p.
- KERSHAW, K. A. 1966. Quantitative and Dynamic Ecology. Edward Arnold (Publishers) Ltd., London. 183 p.
- KOEHLER, A. 1949. Key for the identification of woods without the aid of a hand lens or microscope, 833-838. In Stefferud, Alfred, The Yearbook of Agriculture. United States Department of Agriculture. United States Government Printing Office, Washington, D. C. 944 p.
- KUBÍČEK, F., AND J. BRECHTL. 1970. Charakteristika skupín lesných typov výskumnej plochy IBP v Bábě pri Nitre [Characteristic [sic] of groups of forest types on the IBP research area in Báb near Nitra]. *Biológia* (Bratislava) **25**(1):27-38.
- LEATHERMAN, A. D. 1955. Ecological Life-history of *Lonicera japonica* Thunb. Ph.D. Thesis, University of Tennessee. (Library of Congress Card No. Mic. 55-772). 97 p. University Microfilms. Ann Arbor. Michigan (Dissertation Abstracts **15**(11):1987, Publication No. 15,076).
- LITTLE, S., AND H. A. SOMES. 1967. Results of herbicide trials to control Japanese honeysuckle. U. S. For. Serv. Res. Note NE-62:1-8.
- LJVOV, P. L. 1970. K rasprostraneniyu bukovykh lesov v Dagestane [On the distribution of beech forests in Daghestan]. *Bot. Zh.* **55**(9):1243-1246.
- LUTZ, H. J., AND R. F. CHANDLER, JR. 1946. Forest Soils. John Wiley and Sons, Inc., New York. 514 p.
- MARTIN, A. C., H. S. ZIM, AND A. L. NELSON. 1951. American Wildlife and Plants. Dover Publications, Inc., New York. 500 p.
- MATTHYSSE, J. G. 1959. An evaluation of mist blowing and sanitation in Dutch elm disease control programs. New York State College of Agriculture, Cornell Miscellaneous Bulletin 30. 16 p.
- MCATEE, W. L. 1918. A sketch of the natural history of the District of Columbia. Bull. Biol. Soc. Washington, Number 1. 142 p.
- MITTMAYER, G. 1931. Studien über die Abhängigkeit der Transpiration verschiedener Blatttypen vom Licht und Sättigungsdefizit der Luft. *Jahrb. Wiss. Bot.* **74**(3):364-428.
- NATIONAL CAPITAL PARKS. 1970. Reservation List, January 1, 1970. United States Department of the Interior, National Park Service. 69 p.
- NATIONAL OCEAN SURVEY. 1971. Tide Tables, High and Low Water Predictions, 1972, East Coast of North and South America including Greenland. United States Department of Commerce, National Oceanic and Atmospheric Administration. United States Government Printing Office, Washington, D.C. 290 p.
- NETER, J., AND W. WASSERMAN. 1961. Fundamental statistics for Business and Economics. Second edition. Allyn and Bacon, Inc., Boston. 838 p.
- OLMSTED, F. L., AND J. R. POPE. 1934. (May 16). Draft of preliminary report upon a plan for the permanent development of Roo-

- sevelt Island. 12 p. National Capital Park files.
- OOSTING, H. J. 1956. The Study of Plant Communities. Second edition. W. H. Freeman and Company, San Francisco. 440 p.
- PARADISO, J. L. 1969. Mammals of Maryland. Bureau of Sport Fisheries and Wildlife, United States Department of the Interior. North American Fauna, No. 66. 193 p.
- PENFOUND, W. T. 1966. The role of vines in plant communities. *Advancing Frontiers of Plant Sci.* 17:187-192.
- PERTTULA, U. 1952. Havaintoja järvenkui-  
vatuksen vaikutuksesta vesija rantakas-  
villisuuteen Lempäälässä [Observations  
concerning the influence of a lake-drainage  
on lacustrine and littoral vegetation of  
Lempäälä, S. - Finland.] *Luonnon Tutkija*  
56(4):105-108
- PHILLIPS, E. A. 1959. Methods of Vegetation  
Study. Holt, Rinehart and Winston, Inc.,  
New York, 107 p.
- RAVEN, P. H., AND J. H. THOMAS. 1970. *Iris*  
*pseudacorus* in Western North America.  
*Madroño* 20(8):390-391.
- RUBTZOFF, P. 1959. *Iris pseudacorus* and  
*Caltha palustris* in California. *Leaflets of*  
*Western Bot.* 9(2):31-32.
- STEWART, R. E., AND C. S. ROBBINS. 1958.  
Birds of Maryland and the District of Co-  
lumbia. Bureau of Sport Fisheries and  
Wildlife, United States Department of the  
Interior. North American Fauna, No. 62.  
401 p.
- THOMAS, L. K., JR. 1963. Geomorphology  
and vegetation of Theodore Roosevelt Is-  
land. National Park Service Sci. Rep. No.  
2. 61 p.
- U. S. COAST AND GEODETIC SURVEY. 1970.  
Tide Tables, High and Low Water Pre-  
dictions, 1971, East Coast of North and  
South America including Greenland.  
United States Department of Commerce,  
Environmental Science Services Admin-  
istration. United States Government  
Printing Office, Washington, D.C. 290 p.
- U. S. FOREST SERVICE. 1948. Woody-plant  
Seed Manual. United States Department  
of Agriculture Miscellaneous Publication  
No. 654. 416 p.
- U. S. FOREST SERVICE. 1954. Clearcutting  
raises water level in flatwoods. Southeast  
Forest Experiment Station, Station Paper  
34:17-18.
- U. S. GEOLOGICAL SURVEY. 1965. Wash-  
ington west quadrangle, 7.5 minute series  
(topographic).
- . 1972. Water resource data for Mary-  
land and Delaware - Part 1. Service water  
records. Water Resources Division. Com-  
piled and uncompiled records obtained  
from E. H. Mohler, Chief, Hydrologic  
Data Section.
- U. S. NATIONAL PARK SERVICE. 1968. Mas-  
ter-plan, Theodore Roosevelt Island,  
Washington, D. C. United States Depart-  
ment of the Interior, National Park Ser-  
vice. 52 p.
- WELCH, D. S., AND J. G. MATTHYSSE. 1960.  
Control of the Dutch elm disease in New  
York state. New York State College of  
Agriculture, Cornell Extension Bulletin  
932. 15 p.
- WHIPPLE, S. D., AND K. P. MOECK. 1968.  
Potential uses of Tordon 10K pellets in  
forest management. *Down to Earth* 24(1):  
13-17.
- WILSON, C. L., AND W. E. LOOMIS. 1967.  
Botany. Fourth edition. Holt, Rinehart  
and Winston, New York. 626 p.
- WYMAN, D. 1954. Vines for winter beauty.  
*Plants and Gardens* 10(1):46-50.



# Appendix I

## Statistical References Consulted

- ARKIN, H., AND R. R. COLTON. 1964. Statistical Methods. Fourth edition. Barnes and Noble, Inc., New York. 226 p. and Tables, 48 p.
- BARTLETT, M. S. 1947. The use of transformations. *Biometrics* 3(1):39-52.
- BLISS, C.I. 1967. Statistics in Biology. Volume 1. McGraw-Hill Book Company, Inc., New York. 558 p.
- . 1970. Statistics in Biology. Volume 2. McGraw-Hill Book Company, Inc., New York. 639 p.
- BRADLEY, J. V. 1968. Distribution-free Statistical Tests. Prentice Hall, Englewood Cliffs, N. J. 388 p.
- COCHRAN, W. G. 1953. Sampling Techniques. John Wiley & Sons, Inc., New York. 330 p.
- . 1954. Some methods for strengthening the common  $\chi^2$  tests. *Biometrics* 10(4):417-451.
- CROXTON, F. E. 1953. Elementary Statistics, with Applications in Medicine and the Biological Sciences. Dover Publications, Inc., New York. 376 p.
- , D. COWDEN, AND S. KLEIN. 1967. Applied General Statistics. Third edition. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 754 p.
- DUNCAN, D. B. 1955. Multiple range and multiple F tests. *Biometrics* 11(1):1-42.
- . 1957. Multiple range tests for correlated and heteroscedastic means. *Biometrics* 13(2):164-176.
- EZEKIEL, M. 1924. A method of handling curvilinear correlation for any number of variables. *J. Am. Stat. Assoc.* 19:431-453.
- . 1941. Methods of Correlation Analysis. Second edition. John Wiley & Sons, Inc., New York. 531 p.
- FISHER, R. A. 1937. The Design of Experiments. Second edition. Oliver and Boyd, Edinburgh. 260 p.
- . 1956. Statistical Methods and Scientific Inference. Oliver and Boyd, Edinburgh. 175 p.
- , AND F. YATES. 1953. Statistical Tables for Biological, Agricultural and Medical Research. Fourth edition. Oliver and Boyd, Ltd., Edinburgh and London. 126 p.
- FREESE, F. 1962. Elementary Forest Sampling. Agriculture Handbook No. 232. U. S. Department of Agriculture, Forest Service. U. S. Government Printing Office, Washington, D. C. 91 p.
- . 1967. Elementary Statistical Methods for Foresters. Agriculture Handbook No. 317. U. S. Department of Agriculture, Forest Service. U. S. Government Printing Office, Washington, D. C. 87 p.



- GHISELLI, E. E. 1964. Theory of Psychological Measurement. McGraw-Hill Book Company, New York. 408 p.
- GOULDEN, C. H. 1952. Methods of Statistical Analysis. Second edition. John Wiley & Sons, Inc., New York. 467 p.
- GREIG-SMITH, P. 1964. Quantitative Plant Ecology. Second edition. Butterworths & Company, Ltd., Washington. 256 p.
- HARTER, H. L. 1960. Critical values for Duncan's new multiple range test. *Biometrics* 16:671-685.
- HICKS, C. R. 1965. Fundamental Concepts in the Design of Experiments. Holt, Rhinehart and Winston, New York. 293 p.
- KERSHAW, K. A. 1966. Quantitative and Dynamic Ecology. Edward Arnold, Ltd., London. 183 p.
- KRAMER, C. Y. 1956. Extension of multiple range tests to group means with unequal numbers of replications. *Biometrics* 12(3):307-310.
- LANCASTER, H. O. 1969. The Chi-squared Distribution. John Wiley & Sons, Inc., New York. 356 p.
- MAXWELL, A. E. 1961. Analysing Qualitative Data. John Wiley & Sons, Inc., New York. 163 p.
- MENDENHALL, W. 1971. Introduction to Probability and Statistics. Third edition. Duxbury Press, Belmont, California. 466 p.
- NETER, J., AND W. WASSERMAN. 1961. Fundamental Statistics for Business and Economics. Second edition. Allyn and Bacon, Inc., Boston. 838 p.
- SATTERTHWAITE, F. E. 1946. An approximate distribution of estimates of variance components. *Biometrics* 2:110-114.
- SCHUMACHER, F. X., AND R. A. CHAPMAN. 1954. Sampling Methods in Forestry and Range Management. Third edition. Duke University School Forestry Bull. 7, Durham, N. C. 222 p.
- SEAL, H. L. 1964. Multivariate Statistical Analysis for Biologists. Methuen and Company, Ltd., London. 207 p.
- SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill Book Company, Inc., New York. 312 p.
- SNEDECOR, G. W. 1956. Statistical Methods. Fifth edition. The Iowa State College Press, Ames, Iowa. 534 p.
- , AND W. G. COCHRAN. 1967. Statistical Methods. Sixth edition. The Iowa State University Press, Ames, Iowa. 593 p.
- SPIEGEL, M. R. 1961. Theory and Problems of Statistics. Schaum Publishing Co., New York. 359 p.
- STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co., Inc., New York. 481 p.
- WALSH, J. E. 1962. Handbook of Nonparametric Statistics. Volume I. D. Van Nostrand Company, Inc., Princeton, New Jersey. 549 p.
- . 1965. Handbook of Nonparametric Statistics. Volume II. D. Van Nostrand Company, Inc., Princeton, New Jersey. 686 p.

# Appendix II

## Scientific and Common Names of Plants

Scientific name	Common name
<i>Acer negundo</i>	Boxelder
<i>A. pseudoplatanus</i>	Sycamore maple
<i>A. saccharinum</i>	Silver maple
<i>Acorus calamus</i>	Sweet flag
<i>Allium vineale</i>	Field garlic
<i>Ampelopsis arborea</i>	Pepper vine
<i>Castanea dentata</i>	American chestnut
<i>Claytonia virginica</i>	Spring beauty
<i>Fagus grandifolia</i>	American beech
<i>Fraxinus americana</i>	White ash
<i>F. excelsior</i>	European ash
<i>F. pennsylvanica</i>	Green ash
<i>Hedera helix</i>	English ivy
<i>Impatiens capensis</i>	Spotted touch-me-not
<i>Iris pseudacorus</i>	European yellow iris, yellow flag
<i>Lindera benzoin</i>	Spice bush
<i>Liriodendron tulipifera</i>	Tulip tree
<i>Lonicera japonica</i>	Japanese honeysuckle
<i>Morus alba</i>	White mulberry
<i>Nuphar luteum</i>	Spatterdock, cowlily, yellow water lily, yellow pond lily
<i>Oxalis stricta</i>	Wood-sorrel
<i>Parthenocissus quinquefolia</i>	Virginia creeper
<i>Peltandra virginica</i>	Arrow arum
<i>Podophyllum peltatum</i>	Mayapple
<i>Prunus serotina</i>	Black cherry
<i>Quercus rubra</i>	Northern red oak
<i>Rhus radicans</i>	Poison ivy
<i>Robinia pseudo-acacia</i>	Black locust
<i>Salix caroliniana</i>	Coastal Plain willow, Ward's willow
<i>S. nigra</i>	Black willow
<i>Smilax bona-nox</i>	Bullbrier, greenbrier
<i>Taxodium distichum</i>	Bald cypress

*Tsuga canadensis*  
*Typha angustifolia*  
*T. latifolia*  
*Ulmus americana*  
*Vitis rupestris*

Eastern hemlock  
Narrow-leaved cat-tail  
Common cat-tail  
American elm  
Sand grape

# Index

- Acer negundo* (boxelder), 3, 5, 20, 52  
*Acer pseudoplatanus* (sycamore maple), 64  
*Acer saccharinum* (silver maple), 3, 4  
*Acorus calamus* (sweet flag)  
    competition experiments, 40, 48  
    distribution, 4, 5  
    limiting factor for *Iris*, 65, 69, 70, 76  
*Aix sponsa* (wood duck), 65–67, 69  
*Allium vineale* (field garlic), 20, 37, 53  
American beech. See *Fagus grandifolia*  
American chestnut. See *Castanea dentata*  
American elm. See *Ulmus americana*  
*Ampelopsis arborea* (pepper vine), 56  
Anderson, R. F., 55  
Araliaceae. See *Hedera helix*  
Arnon, D. I., 27  
Arrow arum. See *Peltandra virginica*  
Ash. See *Fraxinus americana*;  
    *Fraxinus excelsior*; *Fraxinus pennsylvanica*  
Atanasiu, L., 62, 64  
  
Bald cypress. See *Taxodium distichum*  
Bartlett, M. S., 7  
Beech. See *Fagus grandifolia*  
Beetle, inner-bark boring. See *Scolytus multistriatus*  
Beetle, native elm bark. See *Hylurgopinus rufipes*  
Billings, W. E., 27  
Black cherry. See *Prunus serotina*  
Black locust. See *Robinia pseudo-acacia*  
Black willow. See *Salix nigra*  
Boxelder. See *Acer negundo*  
  
Boyce, J. S., 55, 61  
Brecht, J., 64  
Brush, W. D., 61  
Bullbrier. See *Smilax bona-nox*  
  
Caprifoliaceae. See *Lonicera japonica*  
*Castanea dentata* (American chestnut), 61  
Cat-tail, common. See *Typha latifolia*  
Cat-tail, narrow-leaved. See *Typha angustifolia*  
Census, 7, 13, 29–30, 46  
*Ceratostomella ulmi* (Dutch elm disease fungus), 55, 61, 63, 75  
Chandler, R. F., Jr., 48, 69  
Chestnut. See *Castanea dentata*  
Chick, W. D., Jr., 55  
*Claytonia virginica* (spring beauty), 5  
Coastal Plain willow. See *Salix caroliniana*  
Cody, W. J., 65  
Collingwood, G. H., 61  
Competition experiments, *Iris*, 12, 23, 24, 38, 40, 48  
Cowlily. See *Nuphar luteum*  
Cypress. See *Taxodium distichum*  
  
Daubenmire, R. F., 55, 62, 72  
Duhamel, J. F., 62  
Duncan, D. B., 8  
Dutch elm disease. See *Ceratostomella ulmi*  
  
Eastern hemlock. See *Tsuga canadensis*  
Ecological dominance, 14–16, 33–35  
Edlin, H. L., 61–63  
Elevation stations, 12  
Elm. See *Ulmus americana*  
Elton, C. S., 71

- English ivy. *See* *Hedera helix*
- Esau, K., 61
- European ash. *See* *Fraxinus excelsior*
- European yellow iris. *See* *Iris pseudacorus*
- Experimental design, 7
- Latin square, 12
  - model I regression, 27, 42
  - paired plots, 9, 16, 36
  - randomized, 9, 13, 16–18, 35, 37, 41–42
- Experimental materials. *See* Elevation stations; Light stations; Quadrat frames; Vegetational strata, stations, placement
- Experiments
- mud deposition, 19
  - plot-weeding, 35
  - verifying, 35–36
- See also* Competition
- experiments; Elevation stations; Experimental design; Germination observations; Habitats studied; Light stations; Quadrat frames; Shade and light experiments; Vegetational strata, stations, placement
- Fagus grandifolia* (American beech), 52, 62
- Fassett, N. C., 65, 69
- Fernald, M. L., 3 (footnote 1), 28, 64, 68
- Field garlic. *See* *Allium vineale*
- Flooding. *See* Limiting factors
- Floodplain, impact of *Hedera helix* on, 58–60
- Forest
- alluvial deposits in, 4
  - See also* Native life forms, replacement of
- Fowells, H. A., 28, 68
- Fraxinus americana* (white ash), 3
- Fraxinus excelsior* (European ash), 64
- Fraxinus pennsylvanica* (green ash), 4, 68
- Friend, D. T. C., 11, 24–25
- Gadgil, M., 60, 70
- Geideman, T. S., 64
- Germination observations, 12
- Iris pseudacorus*, 23, 40, 66, 68
  - Lonicera japonica*, 56
  - Peltandra virginica*, 23, 40
- Gillham, M. E., 68
- Gilluly, J., 71
- Gleason, H. A., 4–5, 28, 37
- Grasovsky, A., 57–58
- Green ash. *See* *Fraxinus pennsylvanica*
- Greenbrier. *See* *Smilax bona-nox*
- Growth rate studies, 16–18, 34–35, 62–63, 72
- Gunning, B. A., 55
- Habitats studied
- description, 8
  - vegetation, 3–4
- Handley, C. O., 55
- Harlow, W. M., 28
- Harrar, E. S., 28
- Hedera helix* (English ivy)
- distribution, 4, 5
  - impact of, 57–64, 72–73, 75–76
  - origin, 4
  - photograph, 33
  - survival, 19, 20
- See also* Ecological dominance; Experiments; Growth rate studies; Habitats studied; Limiting factors; Native life forms, replacement of
- Herbs. *See* Native life forms, replacement of
- History, human. *See* Theodore Roosevelt Island
- Hitchcock, A. S., 65, 70
- Honeysuckle. *See* *Lonicera japonica*
- Hough, R. B., 28
- Hurricane Agnes, effects of, 14, 17–20, 24, 34–36, 59
- Hylurgopinus rufipes* (native elm bark beetle), 55
- Impatiens capensis* (spotted touch-me-not), 6 (photograph), 20

- Iridaceae. See *Iris pseudacorus*
- Iris pseudacorus* (European yellow iris, yellow flag)
- distribution, 5
  - flowering period, 4
  - impact of, 34, 64–71, 73
  - origin, 5, 65
  - replacement of, 21–22, 37–38, 40, 66
- See also Competition
- experiments; Ecological dominance; Germination observations; Habitats studied; Limiting factors
- Ivy. See *Hedera helix*
- Japanese honeysuckle. See *Lonicera japonica*
- Kartaschoff, R., 68
- Kassas, M., 59, 64
- Kephart, L. W., 55
- Kershaw, K. A., 49
- Koehler, A., 61
- Kramer, C. Y., 8
- Kubicek, F., 64
- Land use, past. See Theodore Roosevelt Island
- Leatherman, A. D., 51, 52, 55, 56
- Light
- effect on biomass production, 25
  - effect on community vertical structure, 43
- See also Limiting factors; Native life forms, replacement of
- Light stations, 10–11, 24
- Lily. See *Nuphar luteum*
- Limiting factors
- Elm depopulation, 54–55, 60–63, 72, 75
  - Light, 10, 24–25, 40–42
    - on *Hedera helix*, 42, 57–59, 75
    - on *Iris pseudacorus*, 48, 64–65
    - on *Lonicera japonica*, 42, 75
  - Soil, 32, 48, 68
  - Vegetation, 31, 48
  - Vegetational strata, 27–29, 43–47, 54, 58
  - Water inundation
    - on *Hedera helix*, 75
    - on *Iris pseudacorus*, 30–31, 38, 47–48, 65–66, 69–71, 76
- Lindera benzoin* (spice bush), 20
- Liriodendron tulipifera* (tulip tree), 3, 20, 36, 54, 75
- Little, S., 54, 55
- Little Island, 5
- Ljvov, P. L., 64
- Lonicera japonica* (Japanese honeysuckle)
- distribution, 5
  - impact of, 33–34, 51–57, 71
  - origin of, 20
- See also Ecological dominance; Experiments; Germination observations; Growth rate studies; Habitats studied; Limiting factors; Native life forms, replacement of
- Loomis, W. E., 61
- Lutz, H. J., 48, 69
- Maple. See *Acer pseudoplatanus*; *Acer saccharinum*
- McAtee, W. L., 65
- Marsh, freshwater tidal
- alluvial deposits in, 4
  - destruction of, 65, 67, 69, 70, 71, 76
  - location, 4
  - vegetation, 4–5
- Martin, A. C., 65, 66, 67, 69
- Mason, John, 3
- Matthysse, J. G., 55
- Mayapple. See *Podophyllum peltatum*
- Mittmeyer, G., 59
- Moeck, K. P., 55
- Morus alba* (white mulberry), 3
- Mulberry. See *Morus alba*
- Muskrat. See *Ondatra zibethicus*



- National Capital Parks, 1  
 National Ocean Survey, 4, 24–25  
 Native life forms, replacement of,  
   20–21, 35–37, 51–73  
 Nelson, A. L., 65, 66, 67, 69  
 Neter, J., 30  
 Northern red oak. See *Quercus rubra*  
*Nuphar advena*. See *Nuphar luteum*  
*Nuphar luteum* (spatterdock,  
   cowlily, yellow water lily, yellow  
   pond lily), 4
- Oak, See *Quercus rubra*  
 Olmsted, F. L., 4 (quoted), 4, 62  
*Ondatra zibethicus* (muskrat), 69–70  
 Oosting, H. J., 27, 55, 72  
*Oxalis stricta* (wood sorrel), 20, 36, 53  
 Ozalid type light meter, 6  
   (photograph), 11, 24–25
- Paradiso, J. L., 69, 70  
*Parthenocissus quinquefolia* (Virginia  
   creeper), 20–21, 36–37, 53–54  
*Peltandra virginica* (arrow arum), 31,  
   69, 76  
   distribution, 4, 5, 64  
   germination, 23, 40  
   replacement for *Iris pseudacorus*,  
   37, 66–70  
 Penfound, W. T., 55, 56, 62  
 Pepper vine. See *Ampelopsis arborea*  
 Perttula, U., 69  
 Phillips, E. A., 8  
*Podophyllum peltatum* (mayapple),  
   21, 36, 72  
 Poison ivy. See *Rhus radicans*  
 Pope, J. R., 4 (quoted), 5, 62  
*Prunus serotina* (black cherry), 3, 20,  
   36, 53–54, 75
- Quadrat frames  
   photograph, 6  
   placement of, 9  
   materials used in, 10  
*Quercus rubra* (northern red oak), 3,  
   52, 62
- Random digits table, use of, 8–11, 16,  
   27  
 Raven, P. H., 69  
*Rhus radicans* (poison ivy), 20, 36  
 Robbins, C. S., 66, 67  
*Robinia pseudo-acacia* (black locust),  
   62  
 Rubtsoff, P., 68
- Salix caroliniana* (Coastal Plain  
   willow), 68  
*Salix nigra* (black willow), 4, 68  
 Sand grape. See *Vitis rupestris*  
 Satterthwaite, F. E., 8  
*Scolytus multistriatus* (inner-bark  
   boring beetle), 55, 63  
 Shade and light experiments, 7  
   (photograph), 13, 26–27, 41–42, 58  
 Silver maple. See *Acer saccharinum*  
 Simonov, G. P., 64  
*Smilax bona-nox* (bullbrier,  
   greenbrier), 56  
 Snedecor, G. W., 8  
 Soil. See Limiting factors  
 Solbrig, O. T., 60, 70  
 Somes, H. A., 54, 55  
 Spatterdock. See *Nuphar luteum*  
 Spice bush. See *Lindera benzoin*  
 Spotted touch-me-not. See *Impatiens*  
   *capensis*  
 Spring beauty. See *Claytonia*  
   *virginica*  
 Standley, P. C., 65, 70  
 Stewart, R. E., 66, 67  
 Sweet flag. See *Acorus calamus*  
 Sycamore maple. See *Acer*  
   *pseudoplatanus*  
 Statistical analysis methods, 7  
   arc sine transformations, 15, 17,  
   25  
   chi-square, 8, 13, 17, 19, 22, 28,  
   31–32, 44  
   covariance, 8, 23  
   cross-classified data, 45, 46  
   regression, 8, 29, 31, 41–42,  
   44–45, 48  
   *t* test, 8, 15–19, 25, 28–31

- variance, 8, 15–18, 25, 27–29, 31, 46  
*See also* Random digits table
- Survey designs, 7  
 random sampling, complete, 31  
 random sampling, simple, 14, 27  
*See also* Census; Experimental design
- Taxodium distichum* (bald cypress), 4, 66
- Theodore Roosevelt Island  
 dendrology, 3  
 history, human, 3  
 land use, past, 3, 62  
 location, 1  
 tides affecting, 4  
 topography, 1  
 vegetational disturbances, 3
- Thomas, J. H., 69
- Thomas, L. K., Jr., 1, 3, 4, 5, 62, 66, 67, 70, 72
- Tides. *See* Theodore Roosevelt Island
- Transition areas, 64–65, 67–71
- Tsuga canadensis* (eastern hemlock), 3
- Tulip tree. *See* *Liriodendron tulipifera*
- Typha angustifolia* (narrow-leaved cat-tail),
- Typha latifolia* (common cat-tail), 69
- Ulmus americana* (American elm), 72, 75  
 distribution, 3  
 impact of *Hedera helix* on, 60–64  
 impact of *Lonicera japonica* on, 36, 54  
*See also* Census; *Ceratostomella ulmi*; Native life forms, replacement of
- U.S. Coast and Geodetic Survey, 24–25
- U.S. Forest Service, 66, 68
- U.S. Geological Survey, 1, 31
- U.S. National Park Service, 1, 55, 66
- Vegetational strata  
 depth, 29  
 number, 28  
 stations, placement, 12  
*See also* Limiting factors
- Virginia creeper. *See* *Parthenocissus quinquefolia*
- Vitis rupestris* (sand grape), 20, 36, 56
- Ward's willow. *See* *Salix caroliniana*
- Wasserman, W., 30
- Waters, A. C., 71
- Welch, D. S., 55
- Whipple, S. D., 55
- White ash. *See* *Fraxinus americana*
- White mulberry. *See* *Morus alba*
- Willow. *See* *Salix caroliniana*; *Salix nigra*
- Wilson, C. L., 61
- Wood duck. *See* *Aix sponsa*
- Wood sorrel. *See* *Oxalis stricta*
- Woodford, A. O., 71
- Woody plants. *See* Native life forms, replacement of
- Wyman, D., 64
- Yellow flag. *See* *Iris pseudacorus*
- Yellow pond lily. *See* *Nuphar luteum*
- Yellow water lily. *See* *Nuphar luteum*
- Zim, H. S., 65, 66, 67, 69





